Pseudoasterophyllites cretaceus from the Cenomanian (Cretaceous) of the Czech Republic: a possible link between Chloranthaceae and Ceratophyllum

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DOI: https://doi.org/10.12705/656.8

PALAEOBOTANY

Pseudoasterophyllites cretaceus from the Cenomanian (Cretaceous) of the Czech Republic: A possible link between Chloranthaceae and *Ceratophyllum*

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Keywords angiosperms; *Ceratophyllum*; Chloranthaceae; Cretaceous; paleobotany; *Pseudoasterophyllites*

Supplementary Material The Electronic Supplement (Table S1) and the morphological character matrix (Nexus) are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

Pseudoasterophyllites cretaceus Feistm. ex Velen. is an enigmatic plant best known from the Cenomanian (early Late Cretaceous) of the Czech Republic. It combines reduced simple leaves with characters shared with living early-diverging angiosperm groups, particularly the ambiguously placed families Chloranthaceae and Ceratophyllaceae (*Ceratophyllum* L.). It has simple male flowers consisting of a single stamen containing *Tucanopollis* Regali pollen, which is of interest because it occurs among the earliest angiosperm pollen taxa in the Barremian of Brazil (Regali & al., 1974; Regali, 1989), Gabon and Congo (Doyle & al., 1977; Doyle & Hotton, 1991), Egypt (Schrank & Mahmoud, 2003), England (Hughes, 1994, as Barremian-*ring*), and Spain (R. Zetter, pers. comm.). *Pseudoasterophyllites* Feistm. ex Velen. is unique in the context of other angiosperm taxa in the Cenomanian Peruc-Korycany Formation and the Central European Cretaceous as a whole. However, it is also known from the uppermost Albian (Les Renardières: Kvaček & al., 2012) and the lower Cenomanian (Jaunay-Clan, near Poitiers: Valentin & al., 2014; B. Gomez, pers. obs.) of western France.

The systematic position of *Pseudoasterophyllites cretaceus* has been a matter of debate since the plant was first discovered. It was first collected and designated by O. Feistmantel (1874) as "*Asterophyllites cretaceus*", a nomen nudum implying

Received: 14 Apr 2016 | returned for (first) revision: 20 Jun 2016 | (last) revision received: 18 Sep 2016 | accepted: 18 Sep 2016 || publication date(s): online fast track, 6 Dec 2016; in print and online issues, n/a ||

a relationship to Paleozoic calamites (Equisetales), and first validly published by Velenovský (1887) as *Pseudoasterophyllites cretaceus*. Velenovský interpreted the plant as probably a cryptogamic aquatic but definitely not an equisetalean. Later, Zeiller (1902), during his work on fossil plants from the Barremian of La Pedrera in Spain, described *Pseudoasterophyllites vidali*, now renamed *Montsechia vidalii* (Zeiller) Teixeira. He restudied the original specimens of *P. cretaceus* and interpreted it as a conifer (Zeiller, 1907). By contrast, Velenovský and Viniklář (1926) interpreted the plant as a lycophyte based on reproductive structures that they believed belonged to *P. cretaceus*. More recently, Kvaček & Eklund (2003) suggested that the plant might be a gnetophyte because of its supposedly whorled phyllotaxis. However, prior to this Kvaček (1983: 166) had suggested its probable angiosperm affinities based on cuticle structure. In 2012 Kvaček & al. (2012) provided conclusive evidence for an angiosperm affinity by associating leafy stems in Bohemia and the uppermost Albian of France with stamens that contain *Tucanopollis* pollen, which resembles reticulate-monosulcate pollen assigned to *Clavatipollenites* Couper (Couper, 1958; Doyle & al., 1975; Walker & Walker, 1984) in having supratectal spinules and a sculptured sulcus but differs in having a continuous tectum. Uličný & al. (1997) and Kvaček & al. (2012) interpreted *P. cretaceus* as a halophyte because of its succulent appearance and its occurrence in estuarine facies (Uličný & al., 1997) with a low-diversity plant assemblage dominated by the halophytic conifer *Frenelopsis alata* (K.Feistmantel) Erw.Knobloch (Cheirolepidiaceae).

In the present paper we provide additional evidence for the angiospermous interpretation of *Pseudoasterophyllites* and describe both male and female reproductive organs borne on leafy shoots. In addition, we have incorporated *Pseudoasterophyllites* into a series of phylogenetic analyses, which provide evidence that it belongs near the living families Chloranthaceae and/or Ceratophyllaceae. As with fossils in general, because of the many missing characters, these results are necessarily more or less speculative. However, we consider such analyses far preferable to an intuitive assessment of affinities, and they are essential for integrating fossils into ongoing syntheses of phylogenetic relationships among living plants.

■ MATERIALS AND METHODS

Geological setting. — The plant material described in this paper was collected from the Bohemian Cretaceous Basin in the Czech Republic. It comes from the Peruc-Korycany Formation, the basal-most lithostratigraphic unit of the Basin (Čech & al., 1980; Čech, 2011). Its age is bracketed above by ammonites of the late Cenomanian *Calycoceras guerangeri* and *Metoicoceras geslinianum* zones in the Korycany and Pecínov members of the formation (Čech, 2011). Palynological data indicate a late middle Cenomanian age for these beds (Pacltová, 1977, 1978), and sequence stratigraphic analyses by Uličný & al. (2009) indicate that they belong to the CEN 4 cycle of late middle Cenomanian age. The new material collected in 1993–1995, 2008, and 2015 comes from the Pecínov Quarry near Rynholec (50°08′00″N, 13°54′34″E). Older collections in the National Museum, Prague, are derived from the type locality at Lipenec.

Geological and sequence stratigraphic analyses indicate that the Peruc-Korycany Formation represents a series of paleovalley infills (Uličný & Špičáková, 1996; Uličný & al., 2009). These successions comprise deposits of a variety of continental (braided rivers, meandering streams and floodplains, and anastomosed fluvial systems) and coastal environments (tidally influenced braided rivers, supratidal salt marshes, tidal flats, ebb-tidal deltas, estuaries, and lower shoreface) (Uličný & al., 1997). The studied plant fossils come from mudstone units interpreted at Pecínov as supratidal salt marsh deposits (Uličný & al., 1997; Nguyen Tu & al., 2002). The dominant fossils in these deposits are *Frenelopsis alata* (K.Feistmantel) Erw.Knobloch and *Eretmophyllum obtusum* (Velen.) J.Kvaček (Uličný & al., 1997). Occurrence of these two species and *Pseudoasterophyllites cretaceus* is restricted laterally to isolated, typically monodominant taphocoenoses. Marine influenced habitats are also indicated by palynology (Svobodová in Uličný & al., 1997), namely the occurrence of marine microplankton (e.g., *Micrhystridium* spp.). During excavations in 2015 J.K. observed and collected marine macrofauna even within the layer containing *Pseudoasterophyllites*. All studied material is housed in the National Museum Prague.

Observations on fossils. — Hand specimens were slowly dried. Some were covered by polyvinyl acetate film, while others were conserved in glycerine and later in silicone oil. Part of the material was bulk macerated in a 20% solution of sodium bicarbonate. The best results were achieved when the material was macerated immediately after field work, when it was still wet. These extractions were followed by maceration in 50% hydrofluoric acid. A large portion of the material was sorted by organ, documented, and for final arrangement soaked in alcohol with thymol and stored in plastic boxes with silicone oil. Some specimens, particularly detached leaves and isolated stamens, were macerated several minutes in Schulze's solution, prepared and mounted in glycerine on a preparation glass covered by transparent film (Kvaček, 1999), and examined using an Olympus SZX 12 stereomicroscope. The material for cuticle analysis was prepared using standard techniques (Kvaček, 1999) and observed and documented using an Olympus BX 50 light microscope with a DP digital camera. Part of the material was dried and mounted on stubs for SEM observations using a Jeol JSM-6400 and Hitachi 7000 SEM. Pollen grains were obtained directly from hand specimens or from macerated stamens. Glycerine slides of individual pollen grains were made and the pollen grains were photographed with a Carl Zeiss Axioplan-2 light microscope equipped with a 100× oil immersion objective and a Leica DFC-420 digital camera.

For SEM, individual pollen grains were observed directly in stamens or extracted from macerated stamens, washed in a drop of ethanol and transferred to a piece of film. The film was mounted on a SEM stub (covered with nail polish) and sputter-coated with gold for 3 minutes. The pollen grains were observed and photographed under a Hitachi 7000 SEM and a Tescan Vega-II XMU SEM with an accelerating voltage of 30 kV.

For TEM, individual pollen grains and small parts of macerated stamens were fixed with 2% OsO_4 and embedded in

epoxy resin. The pollen grains were sectioned with a Leica UC6 ultramicrotome. The ultrathin sections were examined under a Jeol 100 B and a Jeol 1011 TEM with an accelerating voltage of 80 kV.

For X-ray microtomography, isolated fruits were mounted on aluminum pin stubs and investigated with a Skyscan1172 Bruker, using an aluminum filter (Al 0.5 mm), voltage 80 kV and current 124 µA. For reconstructions the program NRecon v.16.9.8 was used. Images were obtained, analyzed and manipulated using Avizo v.9.0 and CTvox v.3.0.0 softwares for three-dimensional visualization.

All specimens and preparations are deposited in the paleobotanical collections of the National Museum, Prague.

Phylogenetic analyses. — Phylogenetic analyses used a molecular scaffold approach (Springer & al., 2001), in which a morphological dataset for living and fossil taxa is analyzed with the arrangement of living taxa fixed to a backbone constraint tree. These analyses form several sets that differ in sampling of fossil taxa and assumptions on relationships among living taxa, designed to probe the robustness of the results. We used the dataset of Doyle & Endress (2014), with the addition of a character for solitary female flowers but male flowers borne in inflorescences (scored as unknown in taxa with bisexual flowers) and a few minor corrections in the scoring of extant taxa (see Appendix 1 and online supplementary data). Problems and decisions in scoring of *Pseudoasterophyllites* are discussed in the Results section.

The two backbone trees used are those of Endress & Doyle (2009) and Doyle & Endress (2010, 2014), designated J/M and D&E. These are designed to reflect the range of current hypotheses on the arrangement of the five mesangiosperm clades, which has varied greatly among recent phylogenetic analyses (see Discussion). In both trees, the arrangement of taxa within major clades follows Doyle & Endress (2000), based on a combined analysis of morphological characters and 18S rDNA, *rbcL*, and *atpB* sequences, with additions and subdivisions of taxa and modifications in their arrangement based on more recent molecular analyses (see Soltis & al., 2005; Endress & Doyle, 2009).

Positions of fossil taxa were evaluated by analyzing the dataset of Recent taxa plus one or more fossils using the parsimony program PAUP v.3.0 (Swofford, 1990), with relationships of Recent taxa constrained to one of the backbone trees, with 100 replicates of random addition of taxa and TBR branch swapping. The robustness of inferred relationships and the relative parsimony of alternative arrangements were evaluated by searching for trees various numbers of steps longer than the most parsimonious trees and by moving taxa manually with MacClade v.4.06 (Maddison & Maddison, 2003). We also performed an unconstrained analysis with trees rooted on *Amborella* Baill. Character evolution and character support for relationships were assessed with MacClade. When character states are described as unequivocal synapomorphies of particular clades, this means that the change to this state is unambiguously localized on the branch in question, not necessarily that it occurs only once on the tree. Statements that alternative relationships are "x steps less parsimonious" mean "x steps less parsimonious than relationships in the most parsimonious tree(s)".

■ RESULTS

Taxonomic treatment

Angiospermae

Pseudoasterophyllites cretaceus Feistm. ex Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss. Prag, Math.-Naturwiss. Cl. 1886: 643, fig. 19–25. 1887 – Lectotype (designated by Kvaček & al. in Acta Palaeontol. Polon. 57: 440. 2012): Czech Republic, Lipenec, NMP No. F 654 (National Museum Prague [depicted in Velenovský, 1887: fig. 22]) – **Epitype (designated here):** Czech Republic, Pecínov, NMP No. F 3605c, d (National Museum Prague).

For images of lectotype and epitype, see Fig. 1B and Fig. 1C–F, respectively.

Type stratum. – Peruc-Korycany Formation of the Bohemian Cretaceous Basin, Late Cretaceous, Cenomanian.

Other locality. – Pecínov, Peruc-Korycany Formation, unit 5, Czech Republic.

Material. – Leaves, leafy twigs, twigs: NMP Nos. F 655, 656, 657, 1423, 2279, 2280, 2285, 2898, 2899, 2978, 3605a, b, 3754a, b, 3967–3970, 3972–74, 3982a, 3983a, 3984a, 3985–6, 3989, 3990a, 3991–3a, 3999–4001, 4003–4005, 4044–4069, 4071, 4072, 4073, 4134–4271, 4440–4489, 4513–4516, 4531, 4535, 4536, 4540, 4541, 4548. Fruits and seeds: NMP Nos. F 3754a, b, 3756–3772, 3786, 3976, 3979a, 3980a, 3981, 3988, 4002, 4011–4043, 4070, 4344–4415, 4517, 4518, 4542–4546, 4583. Male inflorescences, stamens: NMP Nos. F 3605e, f, 3755a, b, 3773, 3774, 3971, 3975, 3977–8, 3987, 3997–8, 4003–4005, 4074, 4272–4295, 4320–4343, 4511, 4512, 4534, 4549, 4582.

Emended diagnosis. – Twigs and fruiting axes branching several times. Nodes bearing decussately arranged, opposite leaves. Lateral branches borne in leaf axils, usually in opposite pairs, showing variable internode elongation. Leaves entire-margined, sessile, linear to linear-lanceolate, straight to falcate, keeled, deltoid to finger-shaped, exstipulate with an obtuse apex and a slightly broadened, sometimes auriculate, non-sheathing base. Leaves typically hypostomatic, adaxial cuticle consisting of isodiametric ordinary epidermal cells, abaxial cuticle bearing one or two parallel bands of stomata. Ordinary epidermal cells rectangular to isodiametric, with thick anticlinal walls, in apical part of leaf bearing one centrally placed papilla; stomata predominantly stephanocytic, with exposed guard cells and 8–12 subsidiary cells, less frequently brachyparacytic, oriented transversally or obliquely to the leaf margin.

Flowers unisexual. Female flowers naked and unicarpellate, borne singly in the axil of a leaf/bract on a short stalk, forming a female reproductive unit. Fruit elongated, somewhat curved, indehiscent, with a single locule and one seed. Outer surface of fruit slightly ribbed with rounded apex and sessile stigma surrounding a near-apical short longitudinal slit. Seed pendent, orthotropous, with obliquely placed hilum and tapering micropylar end. Male flowers organized in distinct spicate inflorescences, borne in decussate arrangement in the axils of leaves, formed of various numbers of spirally arranged flowers. Each flower consisting of one stamen subtended by a bract. Stamen consisting of massive anther and very short filament.

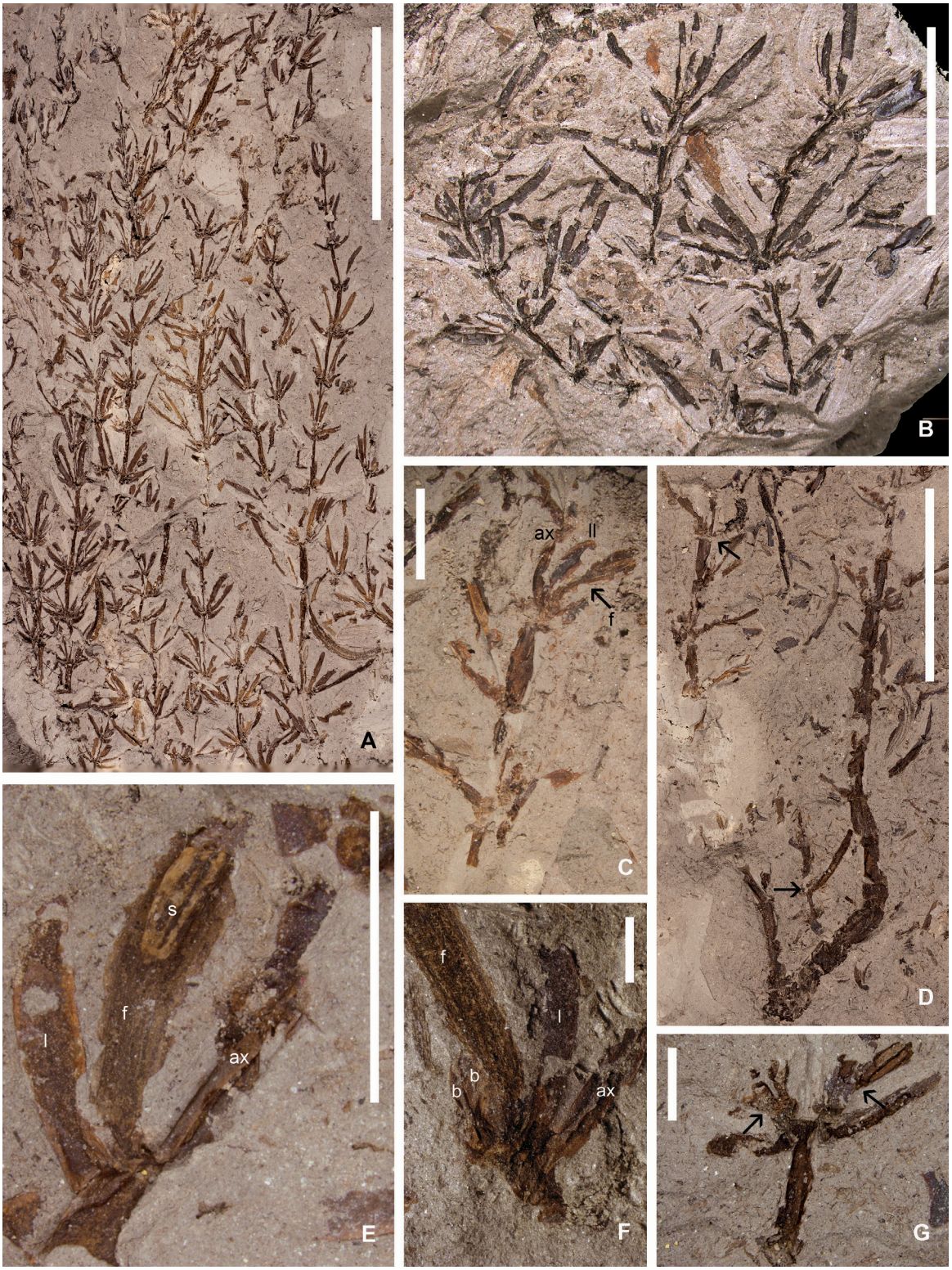

Fig. 1. *Pseudoasterophyllites cretaceus*. **A,** Sterile leafy stems showing arrangement of axes and ultimate shoots, Pecínov, No. F 3605a, scale bar 20 mm; **B,** Lectotype (first depicted in Velenovský, 1887: text-fig. 22), Lipenec, No. F 654, scale bar 10 mm; **C,** Part of epitype, axes (ax) bearing long leaves (ll) and female reproductive unit (f, arrow), Pecínov, No. F 3605c, scale bar 5 mm; **D,** Epitype, counterpart showing three orders of branches and two attached fruits (arrows), Pecínov, No. F 3605d, scale bar 20 mm; **E,** Epitype, female reproductive unit (f) containing seed (s) attached to axis (ax) subtended by a leaf (l), Pecínov, No. F 3605c, scale bar 1 mm; **F,** Detail of epitype, female reproductive unit (f) attached to axis (ax), after careful preparation, with bracts (b) and subtending leaf (l), Pecínov, No. F 3605c, scale bar 5 mm; **G,** Two decussately arranged male inflorescences (arrows) attached to the main axis in axils of leaves, Pecínov, No. F 3605e, scale bar 5 mm.

Anther ovoid-elongate, massive, possessing an expanded connective forming an acute apical extension; tetrasporangiate, each theca with two narrow pollen sacs embedded in tissue of the stamen. Dehiscence by lateral longitudinal slits.

In situ pollen grains monosulcate, globose, with circular equatorial outline. Aperture broad and short, membrane thin and covered by more or less abundant verrucate elements. Tectum continuous except for microperforations, with microechinate to microverrucate supratectal sculpture. Infratectum of mixed columellae and granules, with granules more numerous toward the tectum. Non-apertural nexine less than half as thick as the sexine, consisting of thick, homogeneous foot layer and much thinner and structureless endexine; foot layer thinner and finely lamellate and endexine much thicker under the aperture.

Description — The description is based on several hand specimens and a large amount of mesofossil material from the Pecínov locality. The first part provides a summary of key hand specimens showing the arrangement of branching axes bearing male and female reproductive structures. The second part is devoted to descriptions and measurements of all plant details including female, male, and sterile organs.

The lectotype is a fragment of a leafy stem consisting of six nodes and internodes, with simple linear leaves arranged in an opposite-decussate phyllotaxis. In the axil of each leaf there is a leaf-bearing short shoot with limited growth (Fig. 1B). The lectotype was comprehensively described by Kvaček & al. (2012).

The most instructive hand specimen is F 3605, showing several shoots, both sterile and with female and male reproductive structures. The shoot bearing female reproductive structures is here proposed as an epitype (Fig. 1C–F). It consists of a branched stem, which is leafless in its basal part, bearing twigs of two categories. The main axis is 65 mm long (Fig. 1D), and the secondary branch is 60 mm long. The secondary branch bears several tertiary branches. The epitype shows a stem with several fruits, each of them borne singly (Fig. 1C, E, F). The elongate fruits appear to terminate a short stalk that bears one or two minute bracts (Fig. 1F). Each fruit shows a centrally placed elongate seed.

On the same hand specimen there is preserved a fragmentary axis (F 3605e, f), ca. 8 mm long, bearing leaves and two male inflorescences (Fig. 1G), both of which are borne at the same node (one inflorescence per leaf axil).

Specimen F 4090 shows an impression/compression of a shoot 30 mm long bearing numerous male inflorescences with various numbers of flowers per inflorescence (Fig. 6A).

Specimen F 3605a, b (Fig. 1A), on the same hand specimen as F 3605c–f, shows a group of sterile axes. These axes are more slender and densely placed. The most complete axis is 70 mm long. Each branch bears opposite-decussate leaves with axillary shoots that show varying degrees of development (Fig. 1A). This is the largest specimen of *Pseudoasterophyllites cretaceus* found so far (total dimensions 45 × 150 mm).

Vegetative axes. – The vegetative parts of *Pseudoasterophyllites cretaceus* consist of at least four orders of branched leafy axes. Each axis order develops without interruption, showing monopodial development and indeterminate growth. The lack of bending of the axes appears to indicate a certain rigidity. All nodes except those of ultimate axes produce branches. Branching is decussate and continues along the axes with a branching angle of 20°–50° (Fig. 1A, B). The branches show very short first internodes, suggestive of less immediate (slightly delayed) development compared to that of the axis of the next lower order (Fig. 2K). The length of internodes varies depending on their position on the plant and along the axis, also becoming shorter in the distal parts. The ultimate (highest-order) axes most often are the least developed and show very short internodes. Internode lengths are 0.3–6 mm (Fig. 2H, K). Axis widths vary depending on axis order (ultimate orders are the narrowest) and position along the axis (the distal part is narrower than the basal part). Axis widths in order 1: 4–5 mm, order 2: 1–2 mm, order 3: 0.5–1 mm, order 4: 0.2–0.5 mm (Figs. 1A, D, 2H).

The cuticle of the axes shows polygonal to quadrangular ordinary epidermal cells arranged in rows (Fig. 2L, M). Their size is 15–25 µm wide and 30–50 µm long. The anticlinal walls are 2–7 µm thick. No stomata were observed.

The vegetative parts are heavily leaved. The leaves have an opposite and decussate arrangement. They are entire-margined, simple, unlobed, sessile (with no petiole), and exstipulate. Leaf shape is linear and straight to falcate. The angle of leaf insertion on the stem varies depending on age and position. Younger leaves arise at angles of 15°–30° (Fig. 2E), while older leaves that already have an axillary branch can arise at 90° (Fig. 2H, I). Leaves are preserved flat, usually compressed laterally, being keeled; older leaves are finger-shaped. Their original shape was boat-like (Fig. 3F), as indicated by the shape of leaf scars in 3D-preserved specimens (Fig. 6E). If they are isolated, their original position on the axis is difficult to infer. For orientation we used those leaves with preserved ultimate shoots in their axils (Fig. 2D, G). The leaf base is narrow in more basal leaves (Fig. 2A right, C), broadened to shortly auriculate in more apical leaves (Fig. 2A left, B). Leaf apices are blunt-rounded or sometimes pointed (Fig. 2B). Leaf size varies considerably (1–11 mm long, 0.3–1 mm wide) depending on the position of the leaf on the shoot (Fig. 2A). Small leaves associated with axillary ultimate shoots and male inflorescences are termed short leaves (in contrast to ordinary leaves, termed long leaves). They are deltoid in shape, frequently less than 1 mm long and sometimes even smaller—less than 0.1 mm long (Fig. 2D, F, G). They occur as first leaves of ultimate shoots (Fig. 2D, F, I) and male inflorescences (Fig. 6B, C).

Leaves are typically hypostomatic, with stomata arranged in one or two bands on the abaxial cuticle; however, there are cases of leaves showing stomata on the adaxial cuticle. Isolated leaves may appear to be amphistomatic, but in reality they represent laterally compressed keeled or finger-shaped leaves with one band on each side of the abaxial part of leaf (compare Figs. 2A–C; 3A, F). Stomata in a row are separated by at least three ordinary epidermal cells. Stomata are predominantly stephanocytic, less frequently brachyparacytic, measuring 25–38 × 17.5–25 µm, oriented transversally or more rarely obliquely (Fig. 3F). The stomatal apparatus is level with the epidermis and shows a narrow, pronounced peristomatal rim, a

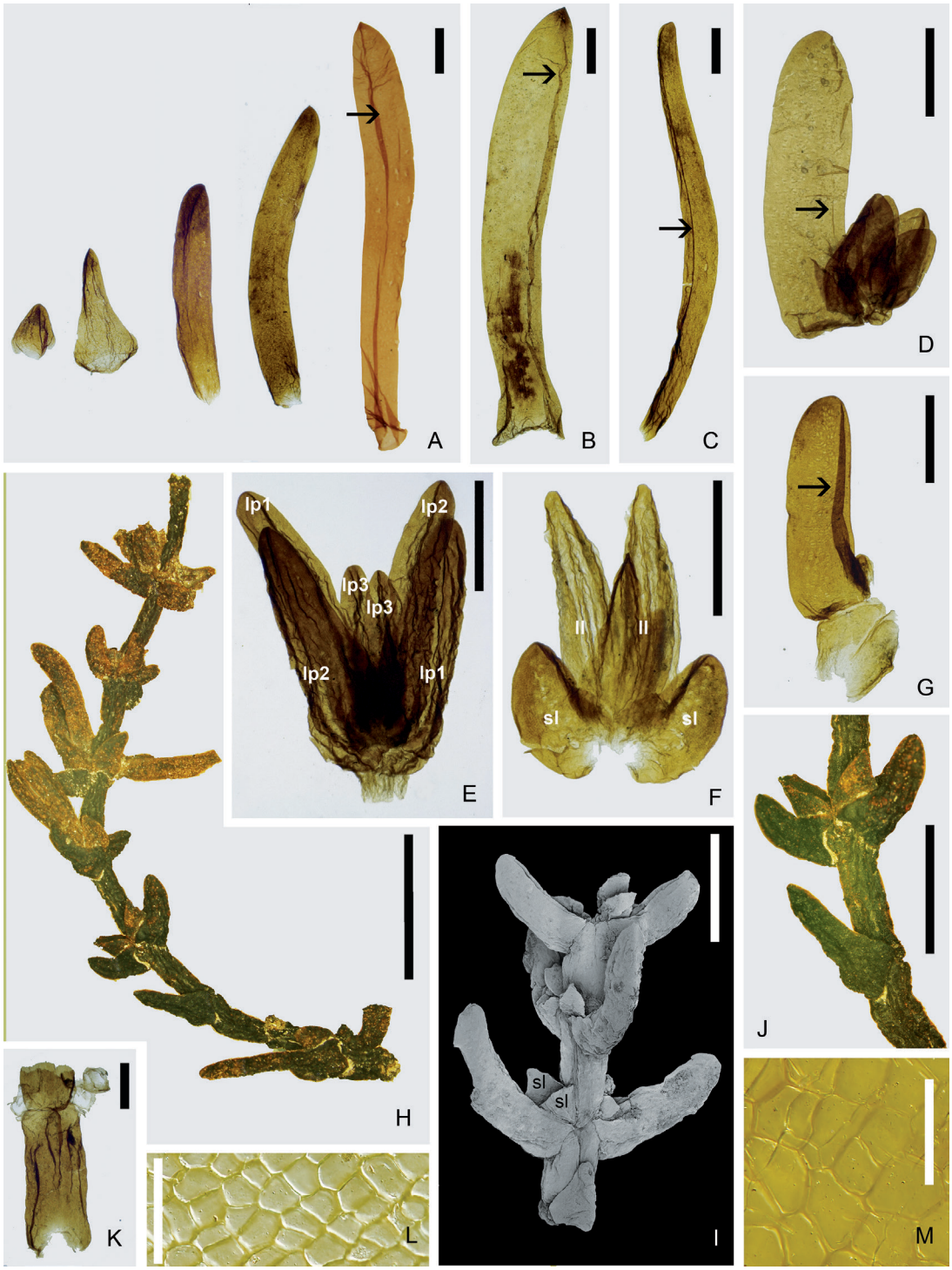

Fig. 2. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Size and shape variation of leaves, from left: No. F 4489, F 4151, F 4142, F 4148, F 4045, arrow at adaxial-abaxial boundary, scale bar 1 mm; **B,** Leaf with auriculate base, No. F 4441, arrow at adaxial-abaxial boundary, scale bar 1 mm; **C,** Leaf with narrow base, arrow at adaxial-abaxial boundary, No. F 4444, scale bar 1 mm; **D,** Leaf with ultimate shoot in its axil, No. F 4463, arrow at adaxial-abaxial boundary, scale bar 1 mm; **E,** Apex of vegetative shoot consisting of three leaf pairs (lp1–lp3), No. F 4437, scale bar 1 mm; **F,** Ultimate lateral shoot showing short leaves (sl) and long leaves (ll), No. F 4438, scale bar 1 mm; **G,** Leaf attached to the main axis with juvenile ultimate shoot in axil, arrow at adaxial-abaxial boundary, No. F 4469, scale bar 1 mm; **H,** Fragment of shoot showing decussate arrangement of leaves, No. F 4514, scale bar 4 mm; **I,** SEM of fragment of shoot showing decussate arrangement of leaves, notice short leaves (sl), No. F 4515, scale bar 1.5 mm; **J,** Detail of H, showing fragment of shoot with leaves in decussate arrangement, No. F 4514, scale bar 2 mm; **K,** Axis with two minute, probably juvenile ultimate shoots borne in its nodal area, No. F 4210, scale bar 1 mm; **L,** Cuticle of ultimate shoot, No. F 4547, scale bar 50 µm; **M,** Cuticle of ordinary axis showing polygonal cells, No. F 3605aA, scale bar 50 µm.

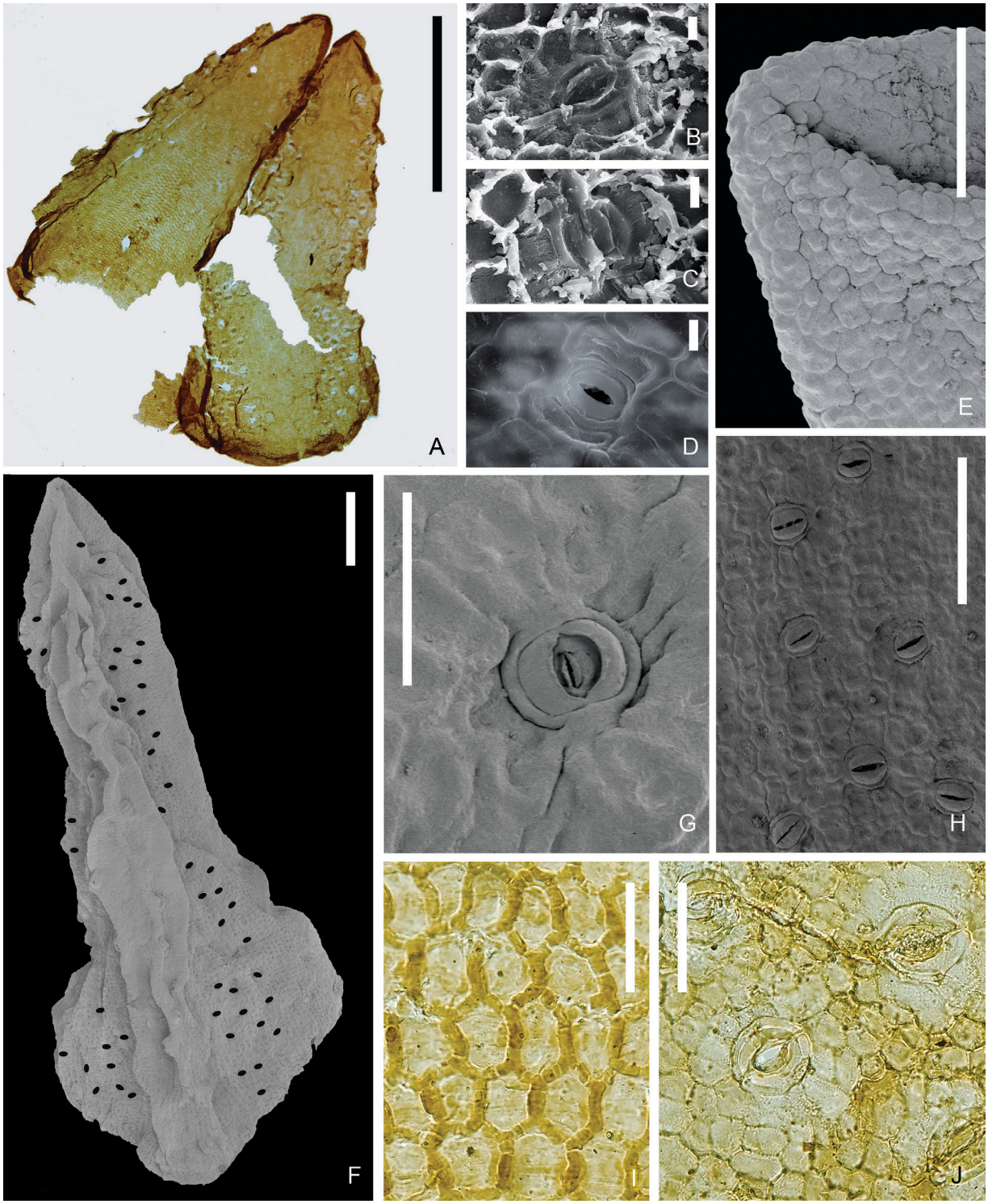

Fig. 3. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Cuticle preparation of small leaf showing two bands of stomata on abaxial cuticle, No. F 4535, scale bar 1 mm; **B,** Inner view of stephanocytic stoma showing subsidiary cells and inner stomatal ledges, SEM, No. F 3605cB, scale bar 10 µm; **C,** Inner view of brachyparacytic stoma, SEM, No. F 3605cB, scale bar 10 µm; **D,** Outer view of brachyparacytic stoma, SEM, No. F 3605cB, scale bar 10 µm; **E,** Apical part of leaf showing external surface of epidermis consisting of ordinary cells with centrally placed papilla, SEM, No. F 4541, scale bar 1 mm; **F,** Abaxial side of keeled leaf showing two bands of stomata (indicated by dark ellipses), detail of Fig. 2H, SEM, No. F 4514, scale bar 300 µm; **G,** Outer view of stephanocytic stoma showing peristomatal rim and inner and outer ledges of guard cells, SEM, No. F 3605cA, scale bar 50 µm; **H,** Outer view of abaxial cuticle showing perpendicular arrangement of stomata, SEM, No. F 4541, scale bar 100 µm; **I,** Adaxial cuticle showing ordinary cells, No. F 4535, scale bar 50 µm; **J,** Abaxial cuticle showing stephanocytic stoma surrounded by 12 subsidiary cells, No. F 4540, scale bar 50 µm.

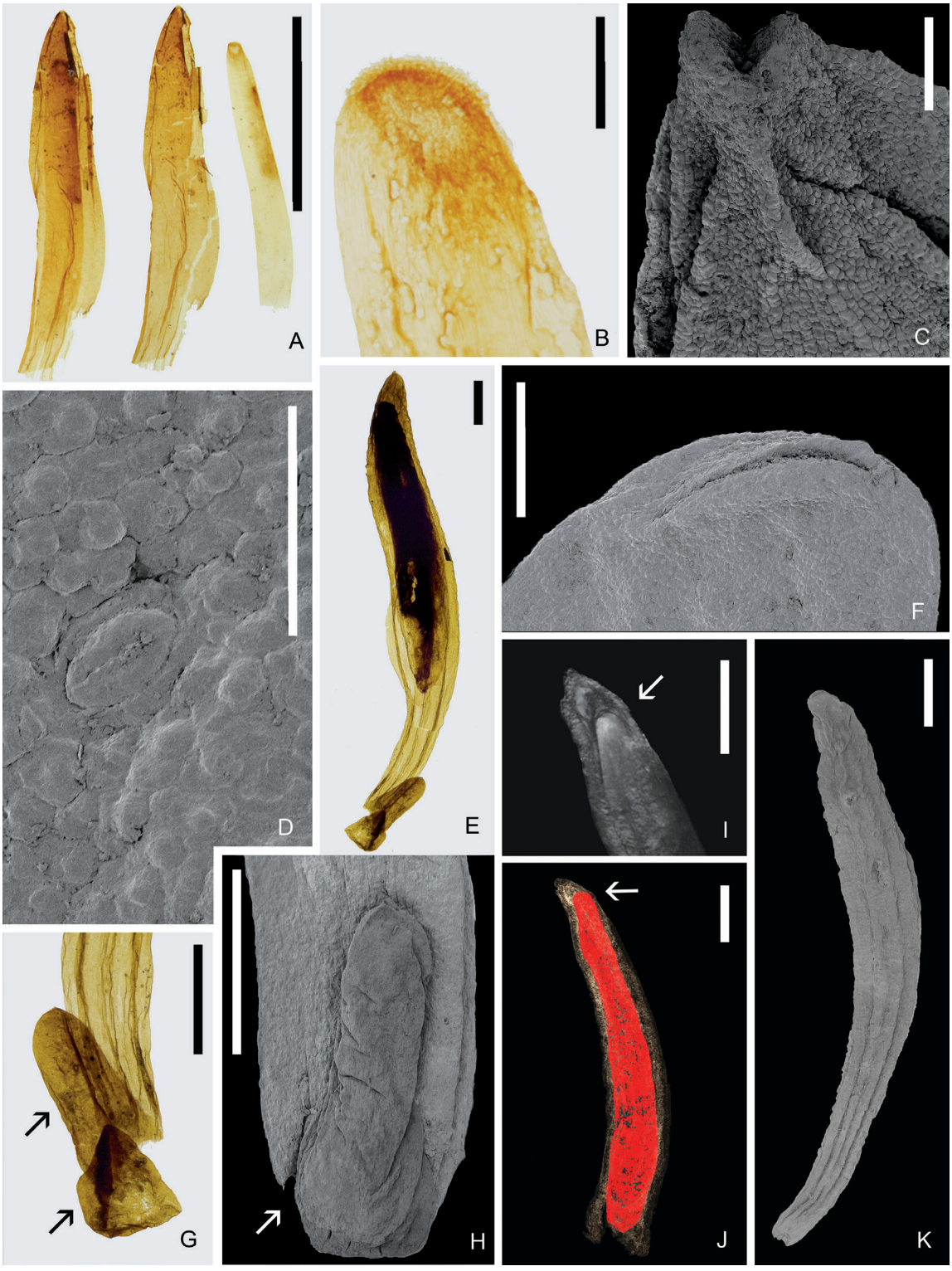

Fig. 4. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Fruit with seed enclosed (left) and extracted (right), No. F 4026a, b, scale bar 0.5 mm; **B,** Detail of A, chalazal region of the seed, No. F 4026a, scale bar 0.5 mm; **C,** Stigmatic area with a short longitudinal slit, No. F 4583, scale bar 0.1 mm; **D,** External epidermal surface of fruit showing papillae and stoma, SEM, No. F 4543, scale bar 50 µm; **E,** Fruit on a stalk bearing two bracts, No. F 4392, scale bar 1 mm; **F,** Stigmatic area with a short longitudinal slit, SEM, No. F 4543, scale bar 0.25 mm; **G,** Detail of E, stalk of the fruit with two bracts (arrows), No. F 4392, specimen inverted, scale bar 1 mm; **H,** Basal part of fruit with stalk (arrow) and bract, SEM, No. F 4544, scale bar 1 mm; **I,** Apical part of the fruit, detail of J, showing chalazal region (arrow), microCT image, No. F 4518, scale bar 1 mm; **J,** Longitudinal section of the same fruit showing position of seed (in red) and its attachment, microCT image, No. F 4518, scale bar 1 mm; **K,** Fruit showing ribbed surface and narrow base, SEM, No. F 4545, scale bar 1 mm.

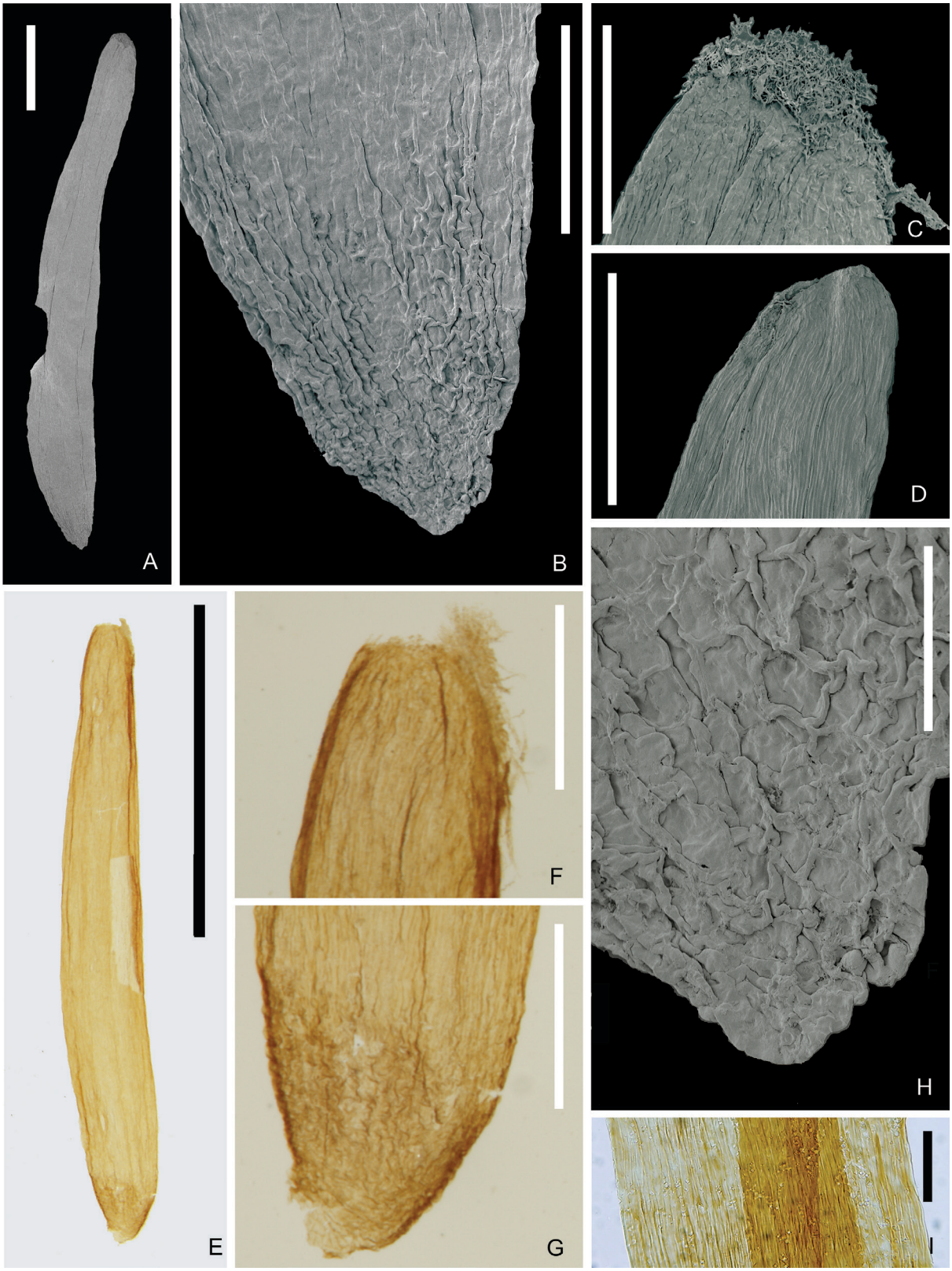

Fig. 5. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Seed with both ends preserved, SEM, No. F 4546, scale bar 1 mm; **B,** Detail of A showing micropylar region of seed, SEM, No. F 4546, scale bar 300 µm; **C,** Detail of A showing chalazal region of seed, SEM, No. F 4546, scale bar 300 µm; **D,** Detail of chalazal part of seed, SEM, No. F 4204, scale bar 100 µm; **E,** Seed showing both ends preserved, No. F 4030, scale bar 3 mm; **F,** Chalazal region of seed, detail of E, No. F 4030, scale bar 0.5 mm; **G,** Micropylar region of seed, detail of E, No. F 4030, scale bar 0.5 mm; **H,** Detail of A showing micropylar region of seed, SEM, No. F 4546, scale bar 100 µm; **I,** Seed cuticle, No. F 4011, scale bar 0.25 mm.

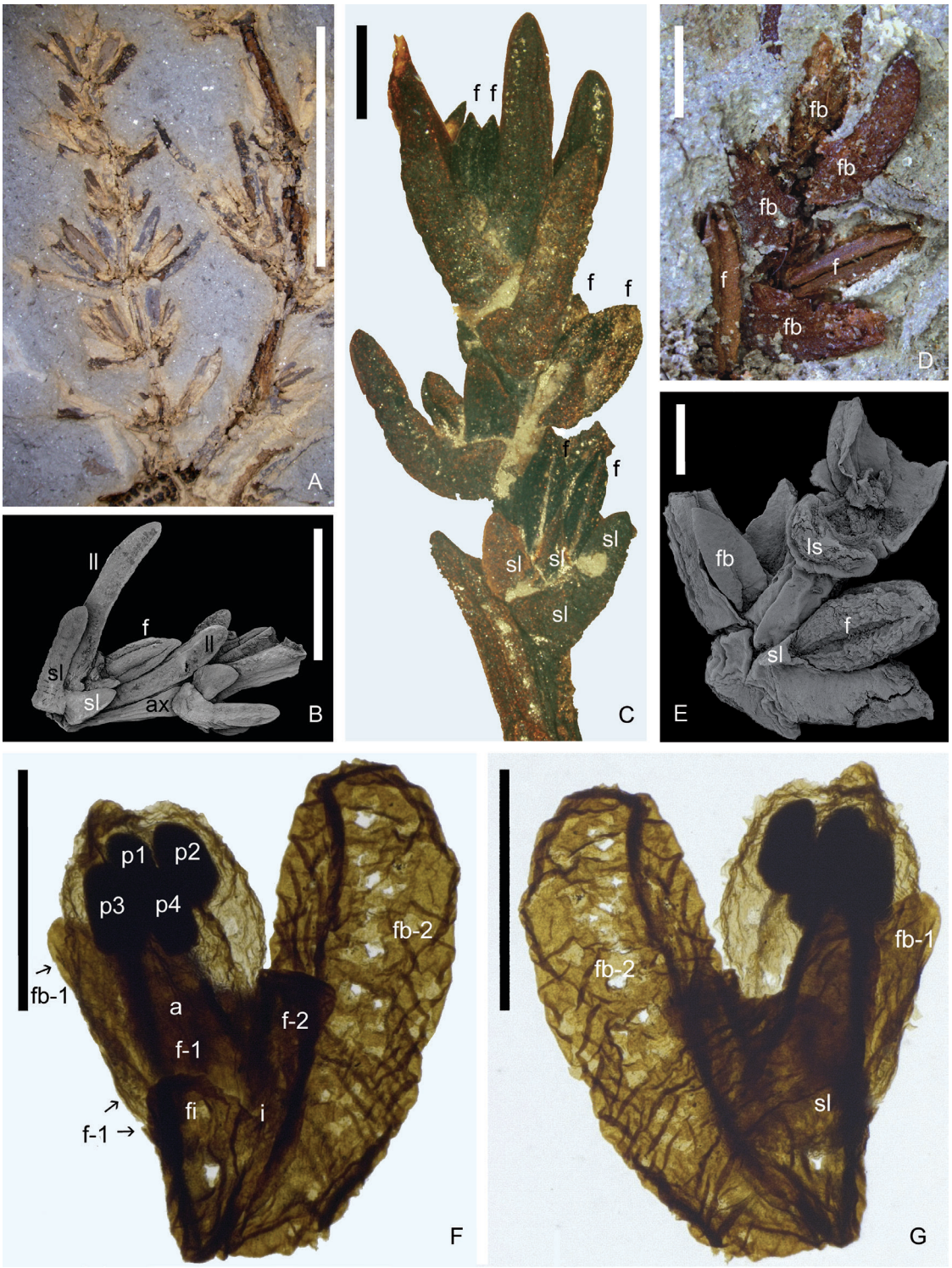

Fig. 6. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Shoot bearing male inflorescences attached to main axis, No. F 4090, scale bar 15 mm; **B,** Shoot bearing male inflorescence with only one flower (f), with first pair of short leaves (sl) and second pair of long leaves (ll) on axis (ax), No. F 4272, scale bar 1 mm; **C,** Shoot bearing three male inflorescences with two flowers (f) each and two pairs of short leaves (sl), No. F 4511, scale bar 1 mm; **D,** Male inflorescence showing five spirally arranged flowers, flower 1 with stamen (st), 2: stamen and flower bract (fb), 3: partially preserved flower bract, 4 & 5: flower bracts, No. F 3773, scale bar 1 mm; **E,** Axis bearing male inflorescence with one flower (f) and one pair of short leaves (sl), notice flower bract (fb) of second, partially preserved inflorescence and well-preserved leaf scar (ls), SEM, No. F 4534, scale bar 0.5 mm; **F & G,** Male inflorescence, view of both sides of preparation, showing inflorescence axis (i), arrangement of two flowers, first flower (f-1) showing filament (fi) and anther (a) with four pollen sacs (p1–p4), second flower (f-2) lacking anther, each flower subtended by a flower bract (fb-1, -2), inflorescence subtended by a short leaf (sl), No. F 4296, scale bar 1 mm.

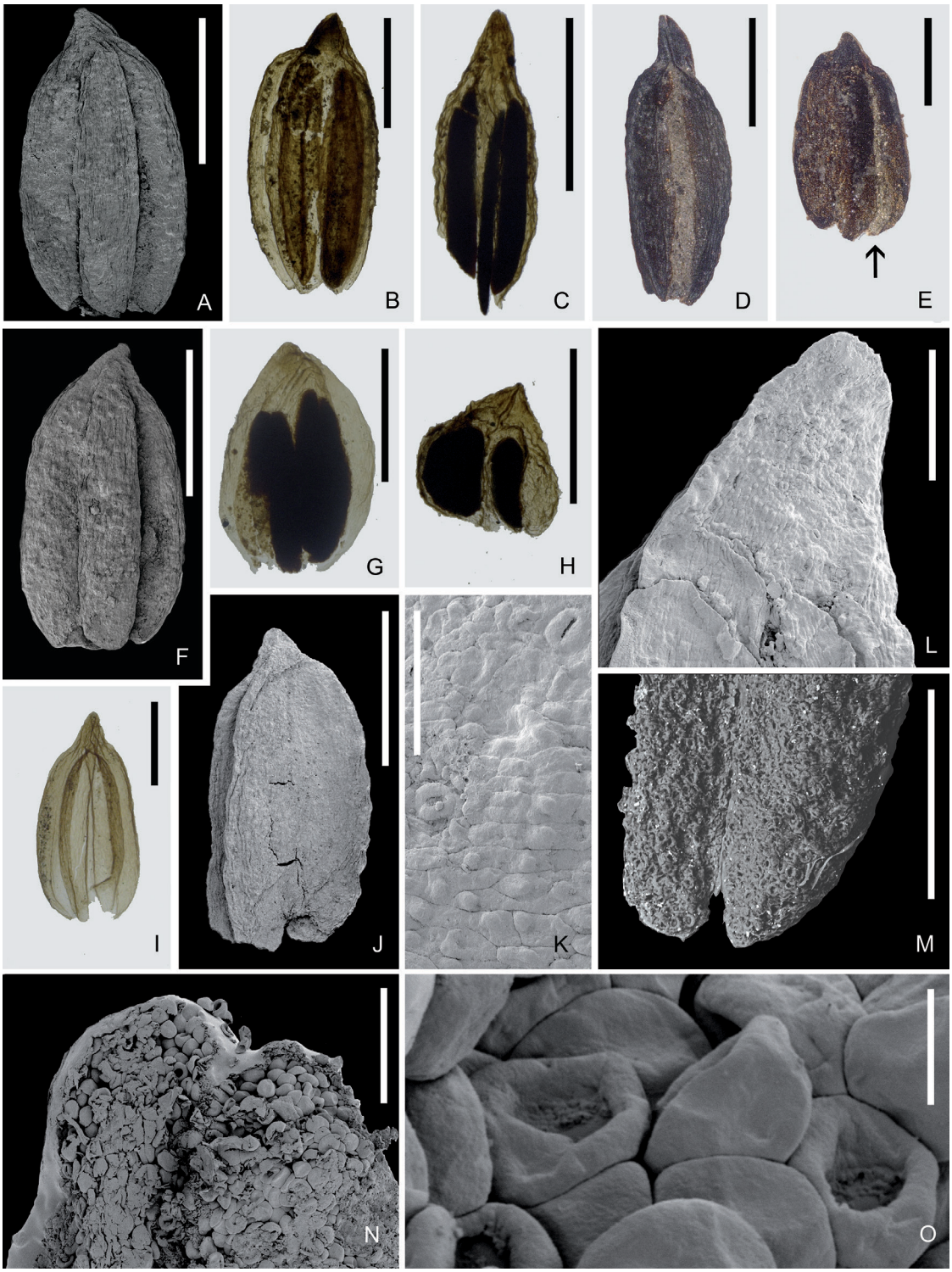

Fig. 7. *Pseudoasterophyllites cretaceus*, Pecínov. **A,** Stamen showing four pollen sacs, No. F 4582, scale bar 1 mm; **B,** Stamen showing four pollen sacs, No. F 4337, scale bar 1 mm; **C,** Stamen showing two thecae and pollen sacs, one of them complete (protruding in basal part), No. F 4308, scale bar 1 mm; **D,** Stamen with pronounced apical projection, No. F 4287, scale bar 1 mm; **E,** Stamen showing dehiscence by lateral slit (arrow), No. F 4293, scale bar 1 mm; **F,** Stamen showing four pollen sacs, No. F 4582, specimen in A inverted, scale bar 1 mm; **G,** Short stamen with short pollen sacs, No. F 4326, scale bar 1 mm; **H,** Very short stamen with short pollen sacs, No. F 4318, scale bar 1 mm; **I,** Empty stamen with no preserved pollen sacs, No. F 4342, scale bar 1 mm; **J,** Stamen showing dehiscence by lateral slit, SEM, No. F 4549, scale bar 0.8 mm; **K,** Epidermis of apical part of stamen showing stomata, SEM, No. F 4548, scale bar 60 µm; **L,** Apical projection of stamen, SEM, No. F 4548, scale bar 0.3; **M,** Detail of isolated theca consisting of two pollen sacs, SEM, No. F. 3773aa, scale bar 0.3 mm; **N,** Broken pollen sac, SEM, No. F 3755a, scale bar 100 µm; **O,** Pollen grains inside stamen, SEM, No. F 3755a, scale bar 10 µm.

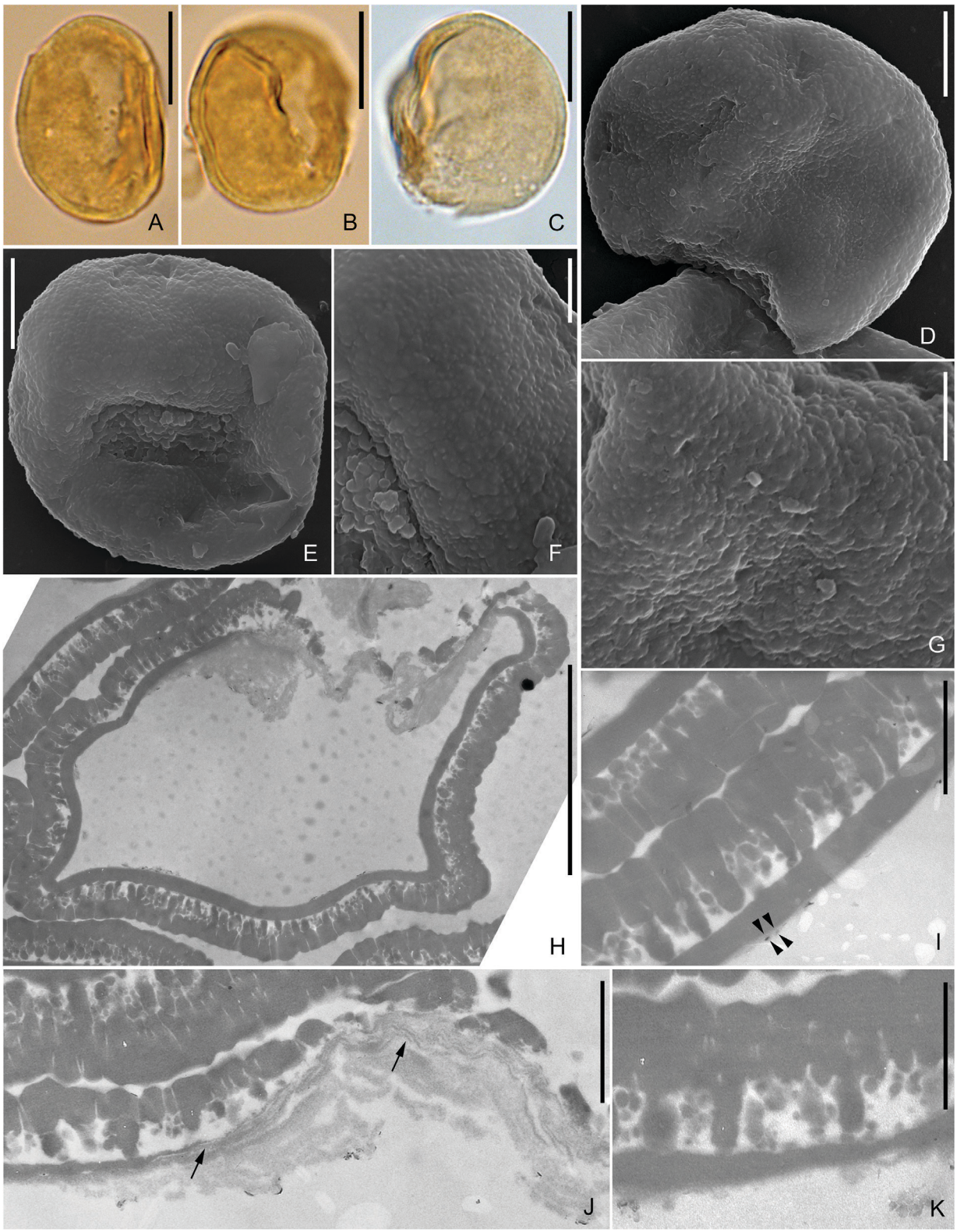

Fig. 8. *Pseudoasterophyllites cretaceus*, Pecínov, pollen grains isolated from and in situ in stamens. **A–C,** LM, three grains in different orientations and focal levels, scale bar 10 µm; **D–G,** SEM; **D,** Equatorial view, sulcus at lower left, scale bar 5 µm; **E,** Near-polar view with sulcus, scale bar 5 µm; **F & G,** Exine sculpture (F: same grain as in E), scale bar 2 µm; **H–K,** TEM; **H,** Section through a whole pollen grain, showing sulcus on upper right, scale bar 5 µm; **I,** Non-apertural region, arrowheads mark borders of less electron-dense endexine, scale bar 1 µm; **J,** Section through aperture in lower of two grains, showing fine ectexinous lamellations (foot layer) in outer nexine (arrows), scale bar 1 µm; **K,** Oblique section in non-apertural region, scale bar 0.7 µm.

prominent vestibule formed by two large outer stomatal ledges of the guard cells (22–35 µm long × 5–10 µm wide) and two inner stomatal ledges (8–20 × 4–6 µm) (Fig. 3B–D, G). Stomatal poles are truncated, cuticular thickening irregularly developed. In stephanocytic stomata, the guard cells are surrounded by 8–12 polygonal to quadrangular subsidiary cells (25–38 µm long × 8–15 µm wide) (Fig. 3B, G, J). Brachyparacytic stomata have two lateral subsidiary cells 20–30 µm long × 9–12 µm wide (Fig. 3C, D).

Ordinary epidermal cells of the abaxial cuticle are isodiametric, polygonal or quadrangular, 7.5–25 µm long × 7.5–20 µm wide (Fig. 3J). Adaxial cuticle shows larger, more elongated cells of similar shape (10–25 × 15–38 µm) (Fig. 3I). The leaf cuticle is 3–7 µm thick. Anticlinal walls are straight or slightly bent. The periclinal walls are covered by small wrinkles, and in terminal and marginal parts of the leaf they bear papillae (Fig. 3E).

Fruits and seeds. – Female reproductive units are best preserved in the epitype (Fig. 1C, E, F). They are borne in axils of leaves on ultimate shoots. Each unit (Fig. 1E, F) consists of a stalk bearing bracts (up to two known) and a single one-seeded fruit (Figs. 1E, F, 9). Fruits, typically occurring isolated, are expanded in the medial part and narrow toward the apex (Fig. 4K). The apex is rounded (Fig. 4F) or sometimes, in smaller fruits, pointed (Fig. 4C). The fruit wall shows a cuticle pattern similar to that of the leaves (Fig. 4D). It consists of isodiametric, quadrangular to polygonal ordinary epidermal cells (12.5–30 µm long × 5–12.5 µm wide) arranged in rows. In the apical part of the fruit the periclinal walls of these cells bear a single low papilla (Fig. 4C, D). Stephanocytic and more rarely brachyparacytic stomata are irregularly scattered on the fruit wall (Fig. 4D). Anticlinal walls of the epidermal cells are straight or bent. In well-preserved specimens (Fig. 4C, F) there is a short near-apical longitudinal slit surrounded by a rim with no discernible papillae, interpreted as stigmatic tissue.

The single seed is elongately ellipsoidal (3–8 mm long × 0.4–0.8 mm wide), sometimes slightly curved (Fig. 5A, E). In rare cases seeds are smaller and more ovoid (1.2–2 mm long and 0.8 mm wide). Most of the seed cuticle shows very elongate cells (5–30 × 60–140 µm) (Fig. 5D, I). Seeds show no sign of a raphe, implying that they are orthotropous, so one end must be chalazal and the other micropylar. Because of variation among seeds (some preservational, some apparently original) and the fact that most seeds are dispersed it was initially difficult to identify the two ends. However, in several cases we were able to establish the polarity of seeds by observing them in situ or dissecting them out of fruits (Fig. 4A, E). The orientation of the seed in the fruit is further confirmed in micro-CT slides (Fig. 4I, J). The end of the seed toward the upper end of the fruit is marked by a more or less dark ring that varies from nearly terminal and symmetrical with the body of the seed (Fig. 5F) to more often laterally displaced (Fig. 4B), and by varying amounts of adhering fibrous material of uncertain composition around or to one side of the ring (Figs. 4B, 5C, F). We interpret this ring as the chalazal attachment scar (hilum); its asymmetry is typical of orthotropous ovules that are attached near the apex of a uniovulate carpel locule, as in *Amborella*, Chloranthaceae, and *Ceratophyllum* (Endress, 2011; Endress & Doyle, 2015). At the opposite end, the seed is often broken (Figs. 1E, 4A), but in several cases it terminates in a conical, sometimes slightly asymmetrical area of wrinkled cuticle (Fig. 5B, G, H), surrounding an opening that we interpret as the micropyle. The seed is therefore orthotropous, with the micropyle pointing downwards; i.e., pendent. We have not been able to determine the original number of integuments.

Male inflorescences and stamens. – Velenovský (1887: fig. 7) described supposed male inflorescences of *Pseudoasterophyllites* from the Lipenec type locality, but careful examination indicates that most of these are male cones of conifers. Our material includes several specimens showing male inflorescences consisting of axes bearing stamens in the axils of bracts. We interpret the entire structure as a spike and each stamen as a male flower.

The male inflorescences correspond to ultimate shoots with two closely spaced basal nodes bearing decussately arranged leaves, as in sterile axes (Fig. 6C). These shoots continue bearing one to five spirally arranged stamens (flowers) (Fig. 6A, D, F, G). Isolated male inflorescences are 1.8–12 mm long and 1.8–4 mm wide (Fig. 4D, F). One specimen (F 4296) shows a small inflorescence with one complete and one incomplete stamen (Fig. 6F, G). The inflorescence is subtended by a short leaf (sl) (see also Fig. 6B, C). Each stamen is subtended by a bract (flower bract; fb-1, -2). The lower stamen (f-1; fi + a) shows an anther (a) with four visible pollen sacs (p1–p4) and a short filament (fi). The upper stamen (f-2) is fragmentary, showing a filament (fi) apparently lacking any anther. Both stamens (flowers) are borne on the inflorescence axis (i), 0.25 mm wide. Larger inflorescences occur embedded in sediment (Fig. 6D). The subtending bracts are elongately obovate, 1–2.5 mm long × 0.5–0.8 mm wide (Fig. 6D, F, G).

Shoots bearing smaller inflorescences were found intact in bulk-macerated material (Fig. 6B, C, E). These inflorescences, borne in the axils of short leaves (sl), show one (Fig. 6B) or two (Fig. 6C) stamens (flowers) per inflorescence. The irregular arrangement of male inflorescences and the variability in shape and number of their organs are paralleled by variation in the presence of short leaves or combinations of short leaves and long leaves in their basal parts (Fig. 6B, C).

The stamens are 1.5–5 mm long and 0.5–2 mm wide. Most of the stamen consists of the anther; the filament is extremely short and inconspicuous (Fig. 6E–G). Shape of the anthers varies from elongately ovoid (Fig. 7A–D) to ovoid (Fig. 7E, G) to shortly ovoid (Fig. 7H). The connective forms an apical extension that varies from very pronounced and claw-like (Fig. 7D) to quite inconspicuous (Fig. 7G). Anthers are tetrasporangiate, consisting of two distinct thecae (Fig. 7A–J) that each contain two narrow pollen sacs (1.0–2.8 mm long × 0.6–1.0 mm wide, Fig. 7C, F, M). The pollen sacs are embedded; i.e., although there may be a pronounced groove between the two sacs making up one theca (Fig. 7E, F), the sacs do not protrude above the level of the area between the two thecae (Fig. 7F, J). The apical connective extension bears the same type of stomata as leaves and fruits (Fig. 7K). Dehiscence is by longitudinal slits, which are lateral in position (Fig. 7E, J).

Pollen. – Pollen is globose in shape (i.e., with a circular equatorial outline) and has a short, wide sulcus (Figs. 7N, O; 8A–E). Size (based on 20 specimens) is 18.3–24.0 µm (average 20.2 µm) as measured in LM, 15.7–23.3 µm (average 19.9 µm) as measured in SEM. Average exine thickness is ca. 1.1 µm as measured in LM. In non-apertural areas, the tectum is nearly continuous, with only very fine microperforations visible in SEM, and bears fine supratectal spinules (microechinae or microverrucae, ca. 8–13 per µm²) (Fig. 8F, G). The sulcus has irregular verrucate sculpture (Fig. 8E, F). Columellae are difficult to resolve with LM in surface view, but they are sometimes visible in optical section (Fig. 8C).

Based on TEM observations (Fig. 8H–K), the tectum is 0.31–0.62 µm (average 0.45 µm) thick. It is traversed by fine microperforations running perpendicular to the surface (Fig. 8I, J). The infratectum is 0.21–0.62 µm (average 0.44 µm) thick. It consists of intergrading columellae and fine granules, with the latter more abundant toward the tectum and sometimes aggregated in short radial rows. The columellae are mostly pendent and not connected with the foot layer (Fig. 8I–K). This infratectal structure corresponds to the "mixed" or "intermediate" type of Doyle (2005) and Doyle & Endress (2014). In the non-apertural areas, the nexine (foot layer plus endexine) is ca. 0.34 µm thick. The foot layer is homogeneous, 0.15–0.44 µm (average 0.29 µm) thick, and is underlain by a thin (0.03–0.07 µm) and structureless endexine, which is less electron-dense than the foot layer (Fig. 8I, K). Toward the aperture the foot layer becomes thinner, while the endexine thickens considerably (Fig. 8H, J). In some specimens the outer part of the nexine contains up to eight fine lamellations; based on electron density these appear to be foot layer (Fig. 8J). The verrucae on the aperture membrane consist of ectexinous globules that appear to pass laterally into the tectum of the surrounding areas.

Fig. 9 presents inflorescence diagrams that summarize our interpretation of the male and female reproductive structures.

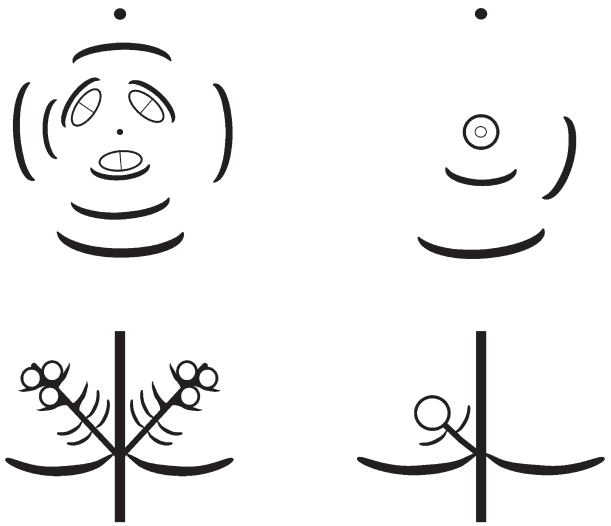

Fig. 9. Inflorescence diagrams showing male and female reproductive structures (above) and schematic lateral views of the same (below).

Comparison with other fossil taxa. — The plant megafossil that is most similar to *Pseudoasterophyllites cretaceus* is *Montsechia vidalii* (Zeiller) Teixeira from much older (Early Cretaceous, Barremian) lacustrine deposits at El Montsec and Las Hoyas in Spain (Gomez & al., 2015) and the late Aptian of Italy (Bartiromo & al., 2012). This similarity was recognized by Zeiller (1902), who originally assigned *M. vidalii* to *Pseudoasterophyllites*. *Montsechia* Teixeira differs in having two distinct architectures that have never been found attached but share the same cuticular features (Gomez & al., 2015). One has alternate-spiral phyllotaxis of branches and tiny leaves borne in short rosettes, while the second shows an opposite-decussate arrangement of much longer, linear leaves. Despite the similar architecture of the long-leaved type of *Montsechia*, its leaves are usually four to five times shorter than those of *Pseudoasterophyllites*. Fruits of *Montsechia* are similar in containing a single pendent, orthotropous seed, but the fruit and seed are much more elongated in *Pseudoasterophyllites*. Unfortunately, neither the male reproductive structures nor the pollen of *Montsechia* are known. Considering its sedimentary context and its even finer leaves and slender flexuous axes, this plant is interpreted as a freshwater aquatic rather than a halophyte (Martín-Closas, 2003; Gomez & al., 2015).

The aquatic plant *Archaefructus* G.Sun & al., from the Barremian-Aptian of China (Sun & al., 1998, 2002), is similar to *Pseudoasterophyllites* in its herbaceous habit and extremely simple flowers. However, it differs in having alternate phyllotaxis, finely dissected leaves, and several ovules per carpel.

Several mesofossil taxa show similarities to *Pseudoasterophyllites*, especially in having uniovulate carpels, although none of these carpels are as elongate as those of *Pseudoasterophyllites*. *Couperites* K.R.Pedersen & al., from the Cenomanian of Maryland (Pedersen & al., 1991), differs in having an anatropous rather than orthotropous pendent ovule, as well as in seed coat anatomy. *Montsechia*, *Appomattoxia* E.M.Friis & al. (Albian, Virginia; Friis & al., 1995), and *Pennicarpus* E.M.Friis & al., the fruits of a plant that produced *Pennipollis* E.M.Friis & al. pollen (Albian, Portugal; Friis & al., 2000), are more similar in having an orthotropous ovule with a laterally displaced dark ring interpreted as a hilar scar at the chalazal end. The carpel of *Appomattoxia* differs conspicuously in being covered with hooked hairs. Friis & al. (2000) interpreted carpels of *Pennicarpus* as having an ascendent (basal) orthotropous ovule. However, Doyle & Endress (2014) argued that its laterally displaced hilar scar, as in modern *Amborella* and Chloranthaceae, is more suggestive of an apically attached ovule, and they therefore scored ovule direction as unknown in their analysis of this taxon (as the *Pennipollis* plant). The spicate male structures associated with *Pennicarpus*, described as *Pennistemon* E.M.Friis & al., differ from those of *Pseudoasterophyllites* in having no bracts subtending the individual stamens (flowers). The *Asteropollis* R.W.Hedlund & G.Norris plant, from the Albian of Portugal (Friis & al., 1999, 2011; Eklund & al., 2004), differs in having three tepals adnate to the carpel, like the living chloranthaceous genus *Hedyosmum* Sw. *Zlatkocarpus* J.Kvaček & E.M.Friis, from the Cenomanian of the Czech Republic (Kvaček & Friis, 2010), also has a vestigial

perianth adnate to the carpel. *Canrightiopsis* E.M.Friis & al., from the Albian of Portugal (Friis & al., 2015), is similar to *Pseudoasterophyllites* in having uniovulate carpels with an orthotropous ovule, but it has bisexual flowers with three stamens adnate to the carpel and pollen of the *Clavatipollenites* type. Another putative relative of Chloranthaceae, *Canrightia* E.M.Friis & K.R.Pedersen, from the Albian of Portugal (Friis & Pedersen, 2011), is more different in having bisexual flowers with a small number of reduced tepals, stamens, and fused carpels. *Donlesia dakotensis* Dilcher & Hong S.Wang, based on spiny uniovulate fruits from the late Albian of the Dakota Formation, U.S.A. (Dilcher & Wang, 2009), which was compared with *Ceratophyllum*, differs from *Pseudoasterophyllites* in its spines, long stylar projection, and long basal stalk.

Comparable in situ and dispersed seeds deserve special consideration. Although *Pseudoasterophyllites* has more elongate seeds than *Appomattoxia* and *Montsechia*, seeds of the three taxa are similar not only in being orthotropous with a laterally displaced hilar scar, but also in having a wrinkled pattern around the micropylar end, a feature not seen in *Pennicarpus*. Dispersed seeds with a similar chalazal scar and micropyle surrounded by wrinkled cuticle were described from the Albian-Cenomanian of Greenland by Miner (1935) as several species of *Spermatites* E.L.Miner and restudied by Batten & Zavattieri (1996), who recognized a thin cuticle overlying the layer of sinuous-walled cells. Batten & Zavattieri (1996) suggested that the inner layer is the cuticle of the nucellus, but because it has an opening at the micropyle it is more likely an inner layer of the integument. The thin outer layer is presumably the cuticle of the outer epidermis.

In most characters visible with LM and SEM, pollen of *Pseudoasterophyllites* resembles dispersed pollen from the Barremian–early Aptian of Brazil that was first described as *Inaperturopollenites crisopolensis* Regali & al. (Regali & al., 1974) and later transferred to *Tucanopollis* (Regali, 1989), "Barremian-*ring*" from the Wealden of England (Hughes, 1994), *Transitoripollis* F.Góczán & Juhász from the Albian of Hungary (Góczán & Juhász, 1984, 1985), and in situ pollen of *Appomattoxia* (Friis & al., 1995). However, the sulcus and the non-apertural areas are less distinct under LM than they are in these forms. *Transitoripollis* is generally smaller (15–18 µm) but similar to pollen of *Pseudoasterophyllites* in having finer spinules and a less sculptured sulcus than the other taxa under discussion. Whether these pollen types are related to each other or form a heterogeneous assemblage is an open question.

TEM shows that the infratectum in *Pseudoasterophyllites* is conspicuously thicker than in *Tucanopollis* from the Barremian of Congo (Doyle & Hotton, 1991) and pollen of *Appomattoxia* (Friis & al., 1995), with longer columellae pendent from the tectum and a larger number of fine granules, but in all three cases the infratectal structure falls within the intermediate (mixed) state recognized in previous analyses. The Czech pollen also has a distinctly thinner nexine than Barremian *Tucanopollis*, *Appomattoxia*, and *Transitoripollis*, as well as the reticulate pollen of fossils identified as *Clavatipollenites* and *Pennipollis* and living members of Chloranthaceae (Doyle & al., 1975; Walker & Walker, 1984; Friis & al., 2000; Eklund & al., 2004), in which the nexine makes up more than a third of the total exine thickness. In having a definite endexine, *Pseudoasterophyllites* differs from Barremian *Tucanopollis*, *Transitoripollis*, *Clavatipollenites*, *Pennipollis*, and modern Chloranthaceae, which have only occasional thin, discontinuous patches of possible endexine. However, *Appomattoxia* also has a thin continuous layer identified as endexine, although this differs from the endexine of *Pseudoasterophyllites* in staining more darkly than the ectexine (Friis & al., 1995). Lamellations are present in the outer part of the apertural nexine in all these taxa.

Pollen associated with vegetative remains and stamens of *Pseudoasterophyllites* in France (Kvaček & al., 2012) differs in some respects from the Czech material. SEM shows that supratectal spinules are less numerous and more prominent in the French material. TEM studies (B. Gomez & V. Daviero-Gomez, pers. obs.) show that it resembles the Czech pollen in the unusual thickness and structure of the infratectum, but the nexine is thicker, as in *Appomattoxia*, Chloranthaceae, etc., and the lamellations under the sulcus are more numerous. Given the similar vegetative and stamen morphology, the thinner nexine in the Czech material may be less significant systematically than might be surmised.

Scoring characters for phylogenetic analysis. — These observations led us to score *Pseudoasterophyllites* for 55 (38.5%) of the 143 characters in the dataset (Appendix 1). We scored several characters of the leaf blade (30–33, 35) as unknown because the leaves lack an appreciable blade, following the procedure used for *Trithuria* Hook.f. (Hydatellaceae, Nymphaeales), which also has reduced linear leaves. We scored inflorescence morphology (42–46) as spikes with floral subtending bracts, based on the male structures, as the more complex sex (as in Endress & Doyle, 2009; Doyle & Endress, 2010, 2014). To these we added a new character (48) for female flowers solitary but male flowers in inflorescences, a condition found only in *Ceratophyllum* among extant taxa, which we scored only in taxa with unisexual flowers. As in other taxa with female flowers lacking a perianth, we scored hypanthium/ovary position (49) as unknown. In the perianth and androecium, the only characters other than morphology of individual stamens (70–77) that could be scored were lack of perianth (54), lack of a calyptrate bract (62), and single stamen (63). Given its shape and the lack of evidence for a ventral suture, the carpel was probably ascidiate, but because this cannot be determined in the absence of developmental or anatomical data, we scored carpel form (98) and sealing (99) as unknown, as for all but a few clearly plicate fossil taxa (Doyle & Endress, 2010). However, a style (102) is clearly lacking. Among characters of the stigma and carpel surface (103–112), only two can be securely determined. We interpret the rim of differentiated cuticle around the slit near the apex of the carpel as an extended stigma (103). Its smoother surface could be due to lack of stigmatic papillae, but because it is possible that there were papillae that had collapsed and were no longer distinguishable in the fruit stage, we have scored stigmatic papillae (105) as unknown. However, the presence of larger stigmatic protuberances (104) can be excluded.

Seed coat characters pose special problems, as they depend on identification of cells derived from the outer epidermis,

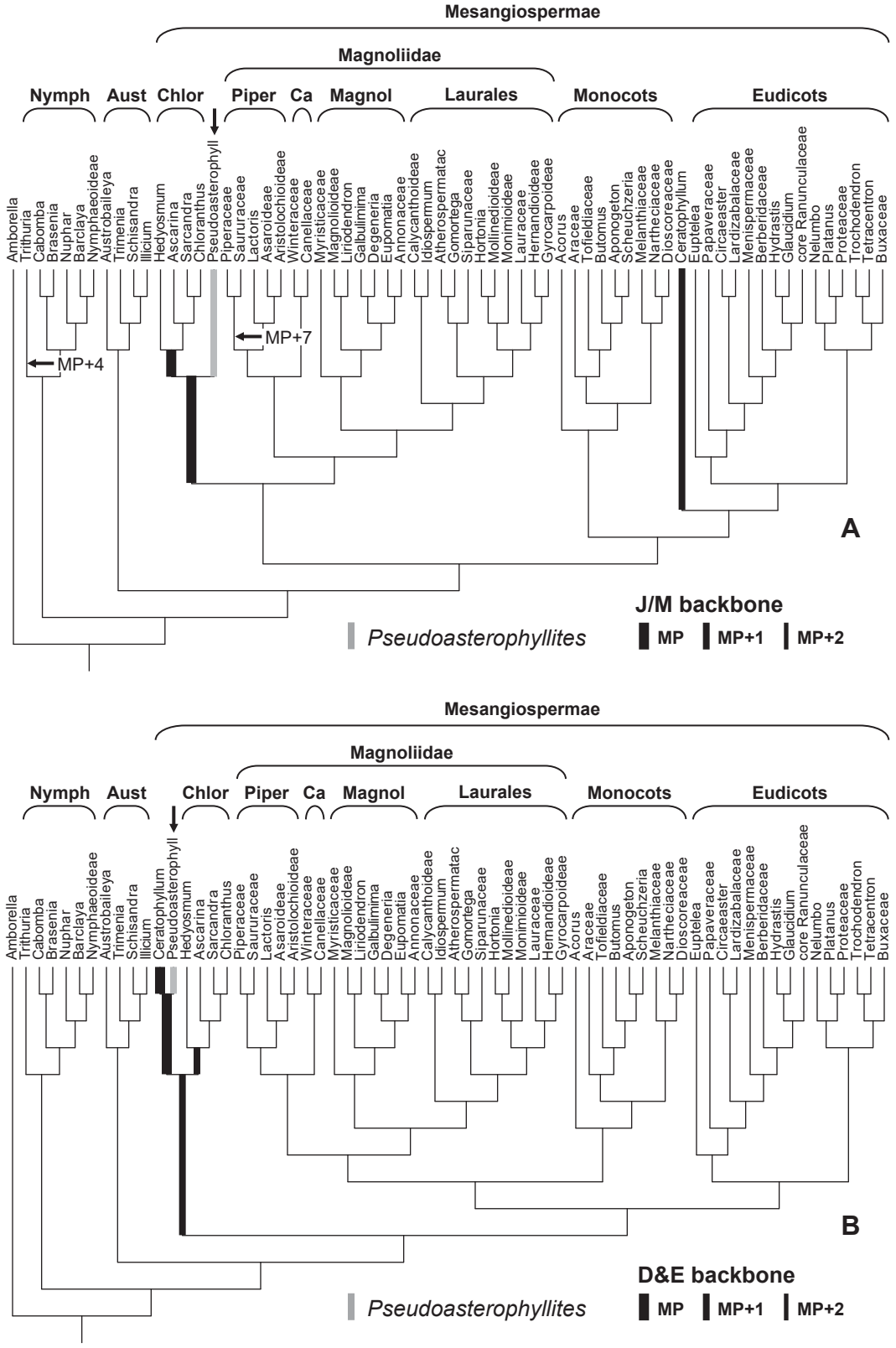

Fig. 10. Results of phylogenetic analyses in which *Pseudoasterophyllites* (arrow) was added alone to two backbone constraint trees of Recent taxa. **A,** Single most parsimonious tree (1034 steps) obtained with the J/M backbone tree; **B,** Single most parsimonious tree (1021 steps) obtained with the D&E tree. Thick lines indicate all most parsimonious (MP), one step less parsimonious (MP+1), and two steps less parsimonious (MP+2) positions for *Pseudoasterophyllites* (no MP+2 positions were found in either analysis). Abbreviations: Nymph = Nymphaeales, Aust = Austrobaileyales, Chlor = Chloranthaceae, Piper = Piperales, Ca = Canellales, Magnol = Magnoliales.

mesophyll, and inner epidermis of each of the two integuments and their mechanical specialization, but this is problematic in taxa with a single integument, which include *Ceratophyllum*, Siparunaceae, and *Circaeaster* Maxim. in the Recent taxon set. It is not known whether *Pseudoasterophyllites* had one integument or two, and the same is true of *Appomattoxia* and the *Pennipollis* plant. However, the wrinkled cuticle around the micropyle in *Pseudoasterophyllites* is closely comparable to the inner layer in *Appomattoxia*, which Friis & al. (1995) compared with the undulate pattern of the inner cuticle in Piperaceae and Saururaceae. In these living taxa this pattern is the result of differentiation of the outer and inner epidermis of the two-layered inner integument into a sclerotic exo- and endotegmen (Corner, 1976). To acknowledge this similarity as a potential synapomorphy, Doyle & Endress (2014) scored *Appomattoxia*, Piperaceae, and Saururaceae as having the same state in their tegmen character (133, state 1: both ecto- and endotegmen thick-walled). However, this character needs redefinition to account for cases in which the ovule may have had only one integument. Assuming that the unitegmic condition most likely originated by congenital fusion of the two ancestral integuments, the outermost and innermost layers of the seed coat as a whole can be identified as the outer epidermis of the outer integument (future exotesta) and the inner epidermis of the inner integument (endotegmen), but other cell layers cannot be defined. For this reason we have redefined state 1 of character 133 in terms of the endotegmen and scored *Pseudoasterophyllites* like *Appomattoxia* in having an undifferentiated exotesta (129, state 0) and an endotegmen of thick-walled cells (133, state 1). This redefinition does not require any change in the scoring of Piperaceae and Saururaceae. Doyle & Endress (2014) scored *Ceratophyllum*, the *Pennipollis* plant, Siparunaceae, and *Circaeaster* as undifferentiated for exotesta and unknown for tegmen, but for consistency we have rescored these taxa as having an undifferentiated tegmen (133, state 0).

Phylogenetic results. — Results obtained when *Pseudoasterophyllites* was added alone to the two backbone trees are shown in Fig. 10. In both cases it has one most parsimonious position, marked by the thickest branch: sister to Chloranthaceae on the J/M tree (Fig. 10A; 1034 steps), sister to *Ceratophyllum* on the D&E tree (Fig. 10B; 1021 steps). Positions that are one and two steps less parsimonious are indicated by branches of lesser thickness. We consider character support for these relationships and the relative parsimony of other positions in the Discussion. An unconstrained analysis, with *Amborella* specified as outgroup to all other living angiosperms, yielded 486 trees (961 steps), in all of which *Pseudoasterophyllites* and *Ceratophyllum* are the sister group of Chloranthaceae.

Results obtained when *Pseudoasterophyllites* was added to the two backbone trees along with *Canrightia*, *Zlatkocarpus*, the *Pennipollis* plant, and the *Asteropollis* plant are presented in Fig. 11. With the J/M backbone, there is one most parsimonious tree (Fig. 11A, 1045 steps), but with the D&E backbone there are three (Fig. 11C–E, 1032 steps).

Results found when *Appomattoxia* and *Pseudoasterophyllites* were added to the backbone trees, with and without the four other fossils, are summarized in Fig. 12. Addition of *Appomattoxia* and *Pseudoasterophyllites* to the J/M backbone resulted in eight most parsimonious trees (Fig. 12A–F; 1039 steps). Their addition to the D&E backbone resulted in one tree (Fig. 12G; 1025 steps). Addition of *Appomattoxia*, *Pseudoasterophyllites*, and the four other fossils resulted in one most parsimonious tree with the J/M backbone (Fig. 12H; 1049 steps), two with the D&E backbone (Fig. 12I, J; 1036 steps).

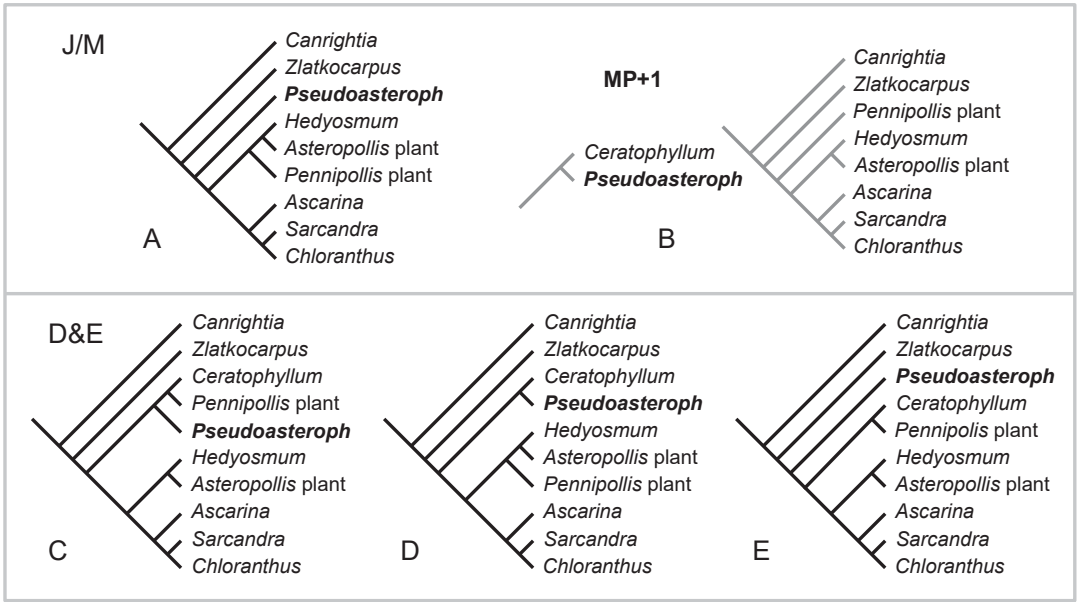

Fig. 11. Arrangements of relevant taxa obtained when *Pseudoasterophyllites* (abbreviated *Pseudoasteroph*) was added to the two backbone constraint trees together with four other fossils that appear related to Chloranthaceae and/or *Ceratophyllum* (*Canrightia*, *Zlatkocarpus*, the *Pennipollis* plant, and the *Asteropollis* plant). **A,** Most parsimonious arrangement obtained with the J/M backbone tree (1045 steps); **B,** Representative of five one step less parsimonious arrangements with *Pseudoasterophyllites* linked with *Ceratophyllum*; **C–E,** Most parsimonious arrangements obtained with the D&E tree (1032 steps).

■ DISCUSSION

Background on Chloranthaceae and *Ceratophyllum*. — Chloranthaceae include four genera of small trees, shrubs, and herbs with extremely simple flowers and an ascidiate carpel containing one pendent, orthotropous ovule (Swamy, 1953; Endress, 1987; Todzia, 1993). *Ascarina* J.R.Forst. & G.Forst. has spikes of unisexual flowers that consist of one stamen (or a few stamens) or one carpel, while *Sarcandra* Gardner has bisexual flowers consisting of only one stamen and one carpel. *Hedyosmum* has male flowers consisting of one stamen, with no subtending bract, but the female flower has three tepals adnate to the ovary. Related fossils were among the most common angiosperms until the rise of tricolpate eudicots in the Albian, including monosulcate pollen with supratectal spinules and a thick nexine (Walker & Walker, 1984), leaves with chloranthoid teeth and cuticles (Upchurch, 1984; Doyle & Upchurch, 2014), and a variety of flowers (Eklund & al., 1997, 2004; Friis & al., 2011). Phylogenetic analyses (Doyle & Endress, 2014) confirm that *Hedyosmum*-like flowers with *Asteropollis* pollen (Friis & al., 1999, 2011; Eklund & al., 2004) are nested within crown group Chloranthaceae (the living clade), linked with *Hedyosmum*, while *Canrightia* (Friis & Pedersen, 2011), a bisexual flower with a vestigial perianth, is a stem relative of the family, and *Zlatkocarpus* (Kvaček & Friis, 2010), which has female flowers with a reduced perianth, may be either nested within the crown group or a stem relative.

Ceratophyllum, the sole living genus of Ceratophyllaceae, is a floating aquatic with whorls of dichotomous leaves and no roots (Les, 1993). The female structures consist of a single uniovulate carpel surrounded by appendages interpreted as bracts; the ovule is pendent and orthotropous, as in Chloranthaceae, but has only one integument. The carpel develops spines in the fruit stage. The male structures have been interpreted as flowers with tepals and many stamens (e.g., Endress, 1994; Iwamoto & al., 2003), but they are more likely spikes of flowers that consist of one stamen with no subtending bracts, surrounded by a basal whorl of bracts (Endress, 2004; Endress & Doyle, 2009, 2015; Doyle & Endress, 2014).

Since 1999 (Mathews & Donoghue, 1999; Parkinson & al., 1999; Qiu & al., 1999; Soltis & al., 1999, 2005), phylogenetic

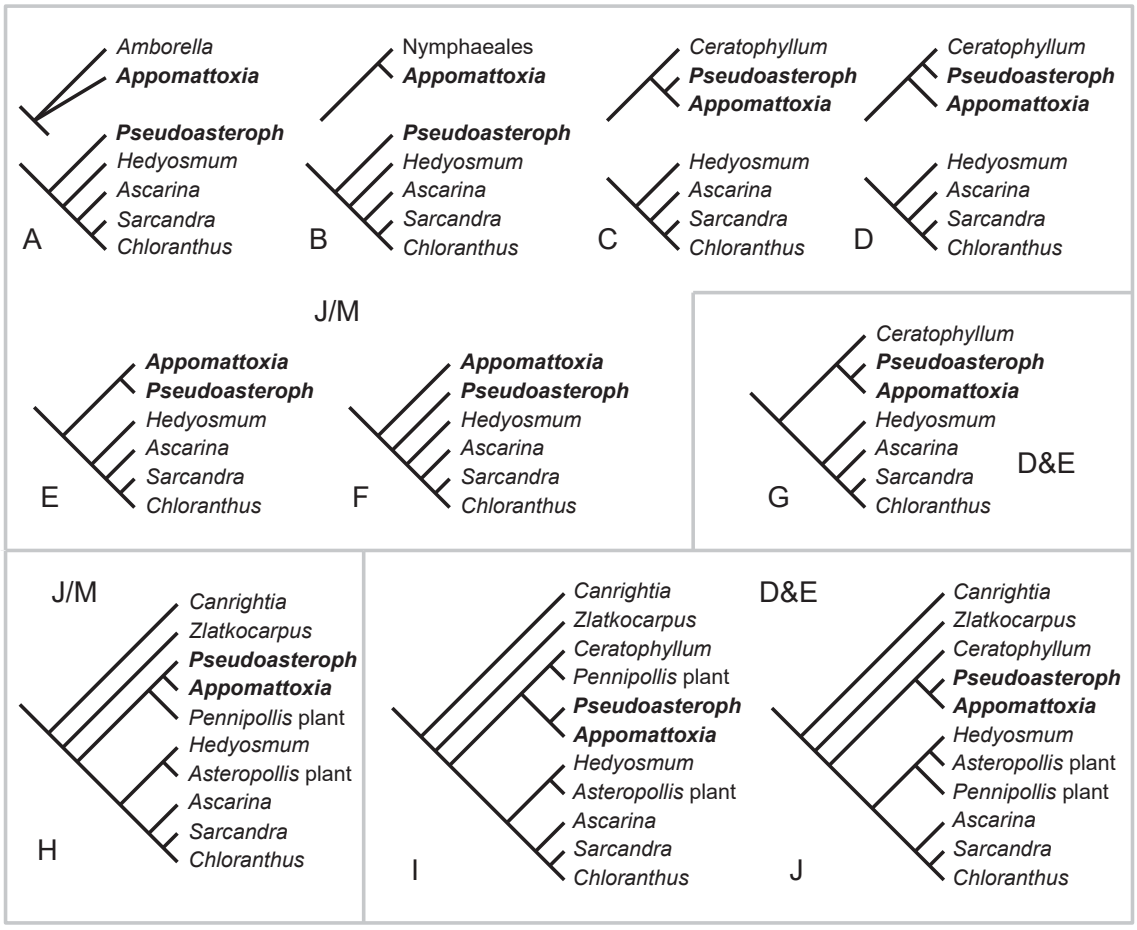

Fig. 12. Results of analyses designed to test a possible relationship between *Pseudoasterophyllites* and the fossil *Appomattoxia*. **A–F,** Arrangements of relevant taxa in most parsimonious trees obtained with addition of *Pseudoasterophyllites* and *Appomattoxia* to the J/M tree (1039 steps; in A, all three arrangments of *Appomattoxia*, *Amborella*, and the remaining angiosperms are equally parsimonious); **G,** Arrangement found with addition of the two fossils to the D&E tree (1025 steps); **H,** Arrangement of relevant taxa obtained with addition of *Pseudoasterophyllites*, *Appomattoxia*, *Canrightia*, *Zlatkocarpus*, the *Pennipollis* plant, and the *Asteropollis* plant to the J/M tree (1049 steps); **I & J,** Arrangements of relevant taxa obtained with addition of the six fossils to the D&E tree (1036 steps).

analyses of angiosperms based on combined sequences of multiple genes have given remarkably consistent results. At the base are the ANITA lines: *Amborella*, Nymphaeales, and Austrobaileyales. The remaining 99.9% of angiosperm species form a clade called Mesangiospermae (Cantino & al., 2007), which consists of eudicots (united by tricolpate pollen), monocots, magnoliids in a restricted sense (Magnoliales, Laurales, Canellales, Piperales), Chloranthaceae, and *Ceratophyllum*. The relationships among these five clades are still not resolved. In trees based on nearly complete plastid genomes (Jansen & al., 2007; Moore & al., 2007), Chloranthaceae are sister to magnoliids and *Ceratophyllum* is sister to eudicots. This is the arrangement in the J/M backbone tree. However, Chloranthaceae and *Ceratophyllum* form a clade in analyses of morphological data (Endress & Doyle, 2009), chloroplast ITS sequences (Antonov & al., 2000), mitochondrial genes (Duvall & al., 2006, 2008; Qiu & al., 2010; Sun & al., 2015), nuclear single-copy genes (Zhang & al., 2012; Zeng & al., 2014; Sun & al., 2015), and genes from the inverted repeat in the plastid genome, thought to be especially reliable because they have a high number of informative sites but low rates of substitution (Moore & al., 2011).

In their morphological analysis, Endress & Doyle (2009) added *Ceratophyllum* to a backbone constraint tree based on an earlier combined morphological and molecular analysis that did not include this genus (Doyle & Endress, 2000). In that tree, Chloranthaceae diverged at the base of the mesangiosperms, in part because they retain ascidiate carpels, like most members of the ANITA lines. When *Ceratophyllum* was added, it was linked with Chloranthaceae, resulting in the D&E backbone tree. Characters that unite *Ceratophyllum* and Chloranthaceae include several related to floral reduction (sessile flowers, one stamen, one carpel), but also opposite or whorled phyllotaxis (treated as one character state) and orthotropous ovule. In terms of the dataset of Endress & Doyle (2009), a sister-group relationship of *Ceratophyllum* and eudicots was at least nine steps less parsimonious, as it is with the present dataset.

Essentially modern *Ceratophyllum*, with whorled dichotomous leaves and spiny fruits, is known from the Eocene (Herendeen & al., 1990), and Dilcher & Wang (2009) described somewhat similar fossils (*Donlesia* Dilcher & Hong S.Wang) from the late Albian Dakota Formation of Kansas. However, for insights on the origin of *Ceratophyllum*, fossils that are related but more plesiomorphic would be more informative. One candidate is the plant noted above with *Pennicarpus* fruits, *Pennistemon* stamens (Friis & al., 2000), and pollen of the *Pennipollis* type, which resembles pollen of Chloranthaceae in having supratectal spinules and a thick foot layer but differs in its unusually coarse reticulum and granular rather than columellar infratectal structure. Friis & al. (2000) interpreted this plant as a monocot, but when Doyle & Endress (2014) added it to the D&E tree, as the *Pennipollis* plant, its most parsimonious position was sister to the *Ceratophyllum*-Chloranthaceae clade, and when they added it to that tree together with *Canrightia*, *Zlatkocarpus*, and the *Asteropollis* plant, one of its two best positions was sister to *Ceratophyllum*. Another possible relative is *Appomattoxia* (Friis & al., 1995), noted for having pollen of the *Tucanopollis* type. Friis & al. (1995) argued that *Appomattoxia* was related to Piperales, based particularly on the similarity of the inner layer of its seed coat to the inner layer in Piperaceae and Saururaceae, but this was not confirmed by Doyle & Endress (2014). When they added *Appomattoxia* alone to both backbone trees, it attached near the basal node of angiosperms, but when they added it to the D&E tree together with *Canrightia*, *Zlatkocarpus*, the *Asteropollis* plant, and the *Pennipollis* plant, one of its four most parsimonious positions was with *Ceratophyllum*, along with the *Pennipollis* plant. Unfortunately pollen of *Ceratophyllum* is uninformative for evaluating such relationships, since its exine is reduced to a thin, featureless layer (Takahashi, 1995).

Addition of *Pseudoasterophyllites* alone to Recent trees. — With the J/M tree (Fig. 10A), in which Chloranthaceae and *Ceratophyllum* are well separated, the most parsimonious position for *Pseudoasterophyllites* is sister to Chloranthaceae. Unequivocally localized synapomorphies of the two taxa are opposite/whorled leaves (21), stephanocytic stomata (36), sessile flowers (lack of pedicel, 45), unisexual flowers (47), one stamen (63), embedded pollen sacs (74), supratectal spinules (92), one carpel (97), and orthotropous ovule (116). *Pseudoasterophyllites* is located below crown group Chloranthaceae because it lacks their sheathing leaf bases (25), stipules (26), thick nexine (96), and stigmatic protuberances (104). Its next best position, which is one step less parsimonious, is sister to *Ceratophyllum*. This is supported by most of the same characters (opposite/whorled leaves, sessile flowers, unisexual flowers, one stamen, embedded pollen sacs, one carpel, orthotropous ovule), plus solitary female flower (48) and no perianth (54). Three positions nested in Chloranthaceae are three steps less parsimonious: sister to *Ascarina*, *Sarcandra*, and *Chloranthus* Sw.; to *Ascarina*; and to *Sarcandra* and *Chloranthus*. Its best position separated from the Chloranthaceae and *Ceratophyllum* lines is with *Trithuria* (Nymphaeales), which is four steps less parsimonious. A position sister to Piperaceae and Saururaceae, which would be supported by sclerotic endotegmen (133), is seven steps less parsimonious.

With the D&E tree (Fig. 10B), in which Chloranthaceae and *Ceratophyllum* form a clade, the most parsimonious position for *Pseudoasterophyllites* is sister to *Ceratophyllum*. Unequivocal synapomorphies of the Chloranthaceae-*Ceratophyllum* clade that are preserved in the fossil are stephanocytic stomata (stomata are absent in *Ceratophyllum*), sessile flowers, one stamen, embedded pollen sacs, one carpel, and orthotropous ovule. The special relationship of *Pseudoasterophyllites* and *Ceratophyllum* is supported by the solitary female flower. As with the J/M tree, Chloranthaceae are united by sheathing leaf bases, stipules, thick nexine, and stigmatic protuberances, plus nexine consisting of foot layer only (95). The next best positions for the fossil, which are one step less parsimonious, are sister to Chloranthaceae or to Chloranthaceae plus *Ceratophyllum*. Its best position outside the Chloranthaceae-*Ceratophyllum* line, with *Trithuria*, is six steps less parsimonious.

Together, these analyses show much stronger support for a relationship of *Pseudoasterophyllites* with Chloranthaceae, *Ceratophyllum*, or both than with any other living angiosperm clade. This perception is also supported by our unconstrained

morphological analysis, with angiosperms rooted on *Amborella*. The resulting trees include many clades found in molecular analyses (e.g., Magnoliales, Laurales, Canellales, Piperales, monocots, Nymphaeales), but they differ in that either Nymphaeales and monocots, Nymphaeales and Piperales, or all three of these taxa (as in the morphological analysis of Doyle & Endress, 2000) form a clade nested in eudicots. In all trees Chloranthaceae, *Ceratophyllum*, and *Pseudoasterophyllites* form a clade, which is attached one node above *Amborella*, on the branch leading to all other angiosperms, and *Pseudoasterophyllites* and *Ceratophyllum* are the sister group of Chloranthaceae.

Addition of *Pseudoasterophyllites* and other fossils to Recent trees. — Studies of Cretaceous mesofossil floras have revealed a remarkable diversity of chloranthoid fossils, several of which have been linked with Chloranthaceae and/or *Ceratophyllum* by phylogenetic analyses (Doyle & Endress, 2014). We know of no reason to believe that this is due to any a priori bias in the analyses. Consideration of these fossils might give a different and more accurate picture of the course of evolution in Chloranthaceae than might be inferred from living taxa alone, and integration of *Pseudoasterophyllites* into this framework might provide improved inferences on its phylogenetic position and character evolution. To evaluate this possibility, we added not only *Pseudoasterophyllites* to the two backbone trees but also the four fossil taxa that were most securely linked with Chloranthaceae and/or *Ceratophyllum* in the analyses of Doyle & Endress (2014): *Canrightia* (Friis & Pedersen, 2011), *Zlatkocarpus* (Kvaček & Friis, 2010), the *Pennipollis* plant (Friis & al., 2000), and the *Asteropollis* plant (Friis & al., 1999, 2011; Eklund & al., 2004).

These analyses are generally consistent with those in which *Pseudoasterophyllites* is added alone to the constraint trees. In the one most parsimonious tree found with the J/M backbone (Fig. 11A), *Pseudoasterophyllites* is sister to crown group Chloranthaceae, above *Canrightia* and *Zlatkocarpus*. Trees in which *Pseudoasterophyllites* is united with *Ceratophyllum* (e.g., Fig. 11B) are one step less parsimonious. In one of the three most parsimonious trees found with the D&E backbone (Fig. 11C), *Pseudoasterophyllites* is sister to *Ceratophyllum* and the *Pennipollis* plant, supported by solitary female flower (not known in the *Pennipollis* plant) and intermediate infratectal structure (88; because this character is ordered, the intermediate state acts as a step toward the granular infratectum of the *Pennipollis* plant). The *Pennipollis* plant is linked with *Ceratophyllum* by loss of bracts subtending the stamens (46) and introrse or extrorse rather than latrorse anthers (76; with male flowers consisting of one stamen with no anatomy and no recognizable floral apex, there are no landmarks to determine whether the pollen sacs are introrse or extrorse: Endress & Doyle, 2009). In the two other trees, *Pseudoasterophyllites* is sister to *Ceratophyllum* alone (Fig. 11D), or to the crown clade including *Ceratophyllum* and Chloranthaceae (Fig. 11E).

Relationship of *Pseudoasterophyllites* and *Appomattoxia*. — The fact that *Pseudoasterophyllites* and *Appomattoxia* both have pollen of the *Tucanopollis* type and similar seed anatomy suggests that they may be related, although they differ in the hooked hairs on the carpel in *Appomattoxia* (as in the eudicot *Circaeaster*), the elongate carpel shape in *Pseudoasterophyllites*, and the relative thicknesses of the exine layers. Unless *Appomattoxia* is related to *Circaeaster*, which is contradicted by pollen and other evidence, its hooked hairs are an autapomorphy and therefore irrelevant for relationships. Comparisons are hampered by the fact that *Appomattoxia* is known from carpels, pollen, and a few isolated stamens (Friis & al., 1995), but its vegetative morphology and the organization of its male structures are unknown. When Doyle & Endress (2014) added *Appomattoxia* by itself to both backbone trees, its four most parsimonious positions were well removed from *Ceratophyllum* and Chloranthaceae, around the basal node of angiosperms and sister to Nymphaeales. However, when *Appomattoxia* was added along with *Canrightia*, *Zlatkocarpus*, the *Pennipollis* plant, and the *Asteropollis* plant, it was associated with Chloranthaceae (J/M) or Chloranthaceae plus *Ceratophyllum* (D&E) in some most parsimonious trees.

The analyses summarized in Fig. 12 were designed to test whether *Appomattoxia* and *Pseudoasterophyllites* are related. In four of the eight most parsimonious trees found when only *Appomattoxia* and *Pseudoasterophyllites* are added to the J/M backbone (Fig. 12A–B), *Appomattoxia* is in any of the three possible positions at the base of angiosperms or sister to Nymphaeales, while *Pseudoasterophyllites* is sister to Chloranthaceae. However, in the four other trees (Fig. 12C–F), both fossils are linked to either Chloranthaceae or *Ceratophyllum*, either as a clade or as two successive outgroups. With the D&E backbone (Fig. 12G), *Appomattoxia* and *Pseudoasterophyllites* form a clade, united by sclerotic endotegmen, that is sister to *Ceratophyllum*. Similarly, *Appomattoxia* and *Pseudoasterophyllites* form a clade when they are added to both backbone trees along with the four other fossils (Fig. 12H–J).

These results do not prove that *Pseudoasterophyllites* and *Appomattoxia* are closely related, but they do indicate that such a relationship is a serious possibility. This underlines the desirability of new data on other characters of *Appomattoxia*. By distantly separating *Pseudoasterophyllites* and *Appomattoxia* from Piperales, all these analyses indicate that the wrinkled inner layer of their seed coat is not homologous with the sclerotic endotegmen of Piperaceae and Saururaceae. Whether the wrinkled layer represents a convergent origin of a sclerotic endotegmen or is derived from a different cell layer cannot be resolved without better anatomical evidence.

The unique morphology of *Pseudoasterophyllites* might suggest that it is an isolated extinct line not closely related to any modern angiosperm group, but this is not supported by our analyses. We see no reason to believe this is due to any bias in the methods, which should be capable of recognizing lineages attached to deep internal branches. A related question is whether *Pseudoasterophyllites* might be an extinct lineage that diverged below the most recent common ancestor of extant angiosperms. Such a position was inferred for *Archaefructus* by Sun & al. (2002) but critiqued by Friis & al. (2003), Doyle (2008), and Endress & Doyle (2009). This possibility is difficult to evaluate directly because the backbone trees include only angiosperms; no outgroups were included

because there is no consensus on the most closely related fossil seed plants (Doyle, 2012). However, even without outgroups it may be possible to infer that a fossil is attached to one of the branches around the basal node, as Doyle & Endress (2014) found when they added *Appomattoxia* alone to the backbone trees, because of its similarities to *Amborella* in characters such as one pendent orthotropous ovule and continuous tectum. By contrast, it is six (J/M) or seven (D&E) steps less parsimonious to place *Pseudoasterophyllites* around the basal node. Because *Pseudoasterophyllites* shares most of the characters that placed *Appomattoxia* near the basal node, this result must be due to other characters, particularly vegetative ones, that conflict with a basal position. Unless fossil angiosperm outgroups are found that share many special features with *Pseudoasterophyllites*, the possibility that it is an angiosperm stem relative will remain purely speculative.

Prospects for future phylogenetic progress. — All these analyses indicate that *Pseudoasterophyllites* is related to Chloranthaceae, *Ceratophyllum*, or both, depending in part on how these living taxa are related to each other. There may be additional synapomorphies that support a special relationship of the fossil to *Ceratophyllum*. For example, given its small stem diameter, it is more than likely that *Pseudoasterophyllites* resembles *Ceratophyllum* in lacking secondary growth. It may also be like *Ceratophyllum* in having only one integument. However, with the present mode of preservation there is no direct evidence on these characters. Similarly, the relatively smooth surface of the area around the apical slit of the carpel may mean that there were no stigmatic papillae, as in *Ceratophyllum*, *Sarcandra*, and *Chloranthus*, whereas papillae are present in *Hedyosmum*, *Ascarina*, and most other potentially related taxa. Better evidence that papillae were absent in the fossil would also strengthen a relationship with *Ceratophyllum*.

An especially significant topic for future analyses is the possible relationship of *Pseudoasterophyllites* and *Montsechia* from the Barremian of Spain (Gomez & al., 2015). In a phylogenetic analysis using the dataset of Doyle & Endress (2014), Gomez & al. (2015) found that the most parsimonious position of *Montsechia* was sister to *Ceratophyllum*, and they assigned it to a new family, Montsechiaceae, in Ceratophyllales. Future analyses, hopefully with the addition of characters of the male structures and pollen of *Montsechia*, may test whether *Pseudoasterophyllites* and *Montsechia* are related to each other and to *Ceratophyllum*, and, if they are, whether they form a clade sister to *Ceratophyllum* or a paraphyletic grade.

Evolutionary and ecological implications. — The crisscrossing similarities of *Pseudoasterophyllites* to Chloranthaceae and *Ceratophyllum* suggest that the fossil may strengthen the hypothesis that the two living groups are related to each other. Whether fossils can affect inferred relationships among extant taxa is a long-standing topic of debate in phylogenetic systematics (Patterson, 1981; Donoghue & al., 1989; O'Leary & al., 2013). With living taxa only (Fig. 13A, B), the D&E tree, in which Chloranthaceae and *Ceratophyllum* form a clade, is 11 steps more parsimonious in terms of morphology than the J/M tree, in which they are distantly separated. However, if *Pseudoasterophyllites* is added to the two trees in its most parsimonious positions (Fig. 13C, D), the tree with Chloranthaceae and *Ceratophyllum* together becomes 13 steps more parsimonious. This indicates that *Pseudoasterophyllites* does indeed increase support for the hypothesis that the two living clades are related, at least by two steps.

One of the trees with five fossils added to the D&E backbone (Fig. 11C) may serve as a framework for a summary of implications for morphological evolution (Fig. 14). A shift to unisexual flowers and reduction to one carpel is inferred after the divergence of *Canrightia*, followed by origin of supratectal spinules after divergence of *Zlatkocarpus*. The most recent common ancestor of the crown clade is reconstructed as having one stamen, but the point where stamen number was reduced is equivocal, since male structures of *Zlatkocarpus* are unknown. If the perianth of *Hedyosmum* and the *Asteropollis*

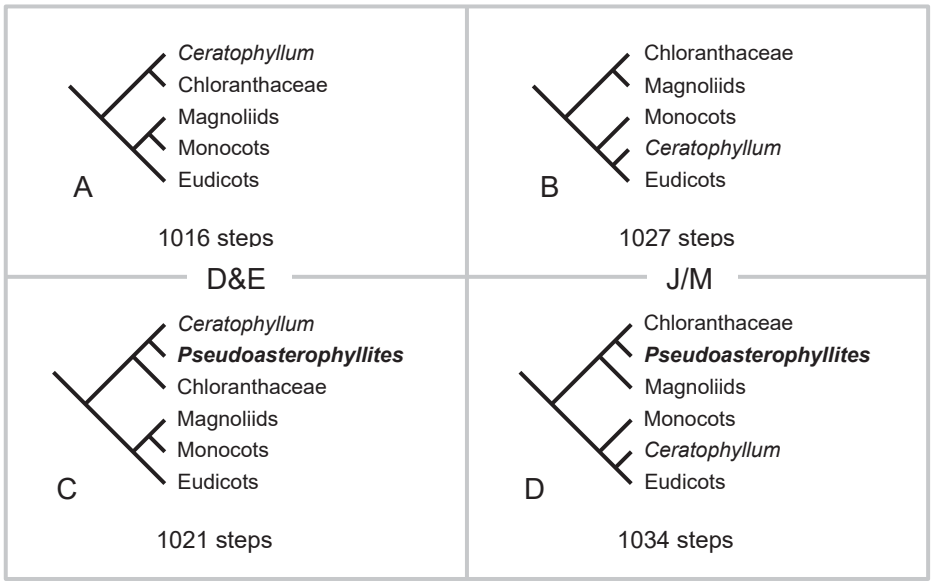

Fig. 13. Testing whether *Pseudoasterophyllites* increases support for a relationship between Chloranthaceae and *Ceratophyllum*. **A & B,** Arrangements of the five major mesangiosperm clades in the D&E and J/M backbone trees; **C & D,** Same two arrangements of mesangiosperm clades with *Pseudoasterophyllites* added in its most parsimonious positions. The D&E arrangement, in which Chloranthaceae and *Ceratophyllum* are sister groups, is 11 steps more parsimonious in terms of morphology than the J/M arrangement, in which the two extant taxa are distantly separated, when only living taxa are considered, but 13 steps more parsimonious when *Pseudoasterophyllites* is added.

plant is retained from lower in the tree, the perianth was lost independently in the clade consisting of *Pseudoasterophyllites*, the *Pennipollis* plant, and *Ceratophyllum* and the clade consisting of *Ascarina*, *Sarcandra*, and *Chloranthus*. On the lineage leading to *Ceratophyllum*, the female inflorescence was first reduced to one flower (this character is not known in the *Pennipollis* plant). The tectum was modified from reticulate to continuous in *Pseudoasterophyllites* (*Tucanopollis*) but became more coarsely reticulate in *Pennipollis*; these divergent changes were superimposed on a trend in infratectal structure from columellar to intermediate (as in *Tucanopollis*) to granular (*Pennipollis*). *Pseudoasterophyllites* still had bracts subtending the stamens, but these were lost in the common ancestor of the *Pennipollis* plant and *Ceratophyllum* (and independently in the *Hedyosmum* line), and anther dehiscence was modified from latrorse to introrse or extrorse. Further specializations in *Ceratophyllum* were loss of the pollen aperture and extreme reduction of the exine (Takahashi, 1995); origin of its peculiar style, which is larger on the presumed ventral side of the carpel (Endress, 1994; Iwamoto & al., 2003; Endress & Doyle, 2015); and dry fruit wall (fleshy in the *Pennipollis* plant, unknown in *Pseudoasterophyllites*). Because vegetative morphology of the *Pennipollis* plant is unknown, it is equivocal whether the linear leaves of *Pseudoasterophyllites* and the dissected leaves of *Ceratophyllum* are autapomorphies of these genera or originated earlier. The same is true for loss of roots and reduction to one integument in *Ceratophyllum*, since data on these characters are lacking in the fossils.

If our phylogenetic results are correct, they have intriguing implications for the early ecological radiation of

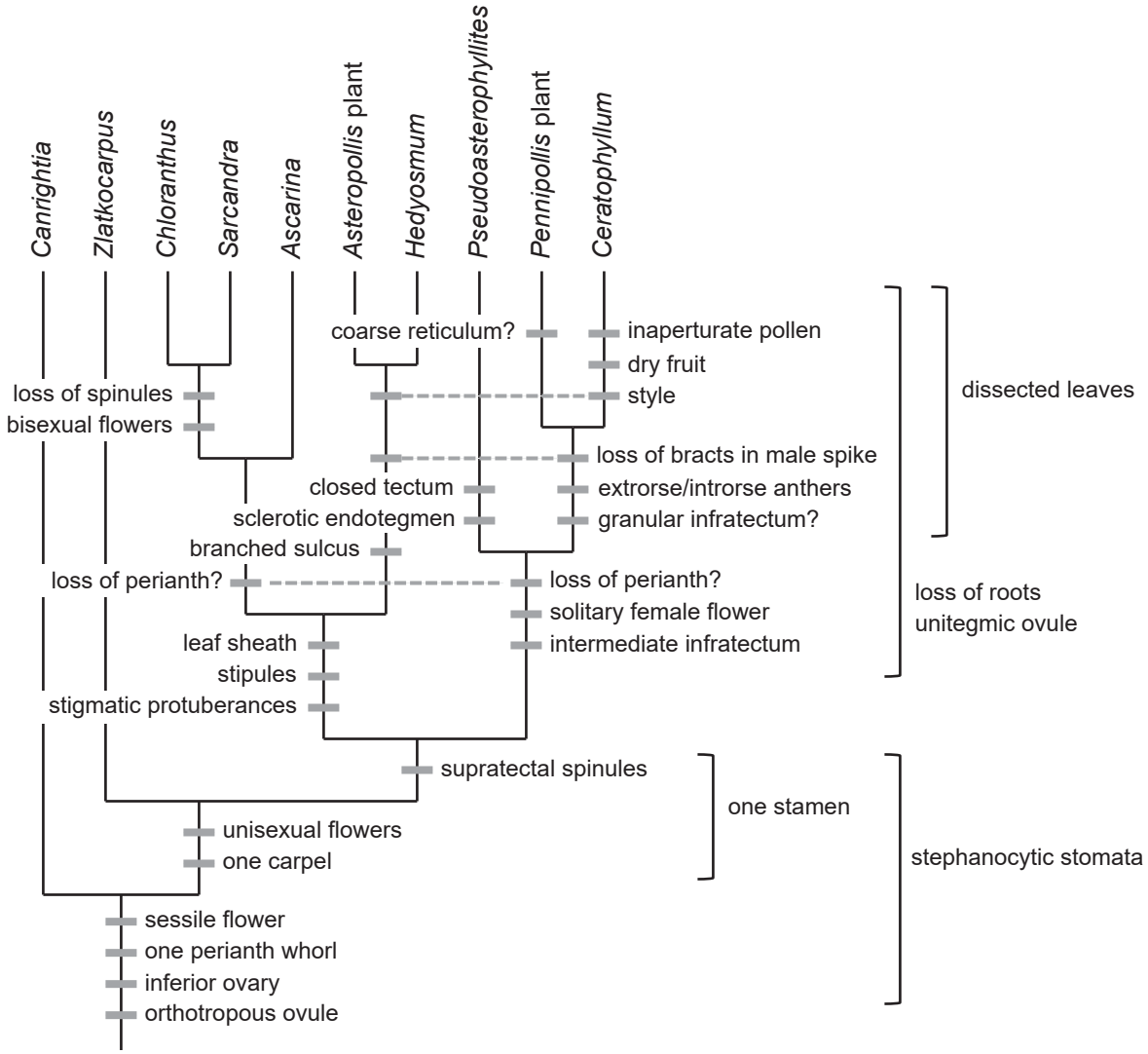

Fig. 14. Inferred evolution of characters discussed in the text in the clade comprising *Ceratophyllum*, Chloranthaceae, and five fossil taxa on the D&E tree (Fig. 10C), based on parsimony optimization using MacClade (Maddison & Maddison, 2003). Gray bars indicate most parsimonious positions for origin of the derived character states (apomorphies) listed. Question marks indicate that the exact position of loss of perianth is equivocal (e.g., it may have been lost twice on the lines to *Ceratophyllum* and the *Ascarina*-*Sarcandra*-*Chloranthus* clade, or once in the common ancestor of *Ceratophyllum* and Chloranthaceae, with a reversal on the line to *Hedyosmum*). Brackets indicate the range of possible positions for origin of the apomorphies indicated, which is uncertain due to incomplete information in fossils.

angiosperms. Except for the aquatic Nymphaeales, members of the ANITA lines, namely *Amborella* and Austrobaileyales, are largely restricted to dark, wet forest understory habitats, where they show various adaptations to disturbance, and this has been reconstructed as the original ecology of angiosperms (Feild & al., 2004, 2009). Chloranthaceae are physiologically adapted to open disturbed sites as well, which has been suggested as an explanation for their early success and worldwide distribution in the Early Cretaceous (Feild & al., 2004; Doyle & Endress, 2014), and *Ceratophyllum* invaded aquatic habitats. Whether or not the reconstruction of the ancestral angiosperm ecology is correct, *Pseudoasterophyllites* suggests that the Chloranthaceae-*Ceratophyllum* clade occupied more diverse habitats than might be imagined from considering its relict modern members. As argued by Kvaček & al. (2012), the estuarine sedimentary context and the apparent succulent character of *Pseudoasterophyllites* (reflected in the curiously uneven thickness of the stem in Fig. 1D) suggest that it was a halophyte.

If the plants that produced *Tucanopollis* pollen were related, which is not established, these results also provide a new perspective on the abundance of *Tucanopollis* in the Early Cretaceous of Northern Gondwana (originally described as *Inaperturopollenites crisopolensis* by Regali & al., 1974; Doyle & al., 1977; Regali, 1989; Doyle & Hotton, 1991), where it was probably the most common angiosperm pollen in the Barremian. Since Brenner (1976), the climate in this tropical zone has been interpreted as more or less arid through the Barremian-Albian interval, as inferred from the presence of thick salt deposits in the Aptian of the South Atlantic rift, the absence or scarcity of coals, the low abundance of spores, and the dominance of *Classopollis* (representing the xeromorphic conifer family Cheirolepidiaceae) and ephedroid pollen (Gnetales), except for wetter conditions in the Middle East and other areas near the paleoequator (Doyle & al., 1982; Brenner, 1996). If the plants that produced Barremian *Tucanopollis* pollen were like *Pseudoasterophyllites*, their most likely habitats in this region might be local lacustrine and/or saline environments in lowland floodplains and deltas.

These considerations highlight how useful it would be to discover vegetative remains of the plants that produced Early Cretaceous *Tucanopollis* pollen, as well as potentially related groups known only as flowers and pollen, such as *Appomattoxia* and the *Pennipollis* plant. Such information could strengthen or refute the hypotheses that we have presented.

■ ACKNOWLEDGEMENTS

We thank Hervé Sauquet and Kevin Nixon for pointing out problems in scoring characters of flowers in Hernandiaceae and leaves in *Platanus* and Proteaceae, Zlatko Kvaček and Gary Upchurch for discussion of stomatal morphology, and two anonymous reviewers for critical comments that led to improvements in the manuscript. Jaromír Váňa, Lenka Váchová, Zuzana Heřmanová and Valeria Vaškaninová (all National Museum Prague) are gratefully acknowledged for their assistance with preparation and documentation of the mesofossil material. J.K. was supported by Czech Grant Agency (project No. 15-049875). Funding for B.G. and V.D.-G. was provided by Unité Mixte de Recherche 5276 of Centre National de la Recherche Scientifique; Projects CGL2013-42643-P, CGL2015-68363-P and CGL2015-60805-P of the Ministerio de Economía y Competitividad of the Spanish government and Project 2014SGR-251 funded by the Catalan government. M.T. was supported by the Russian Foundation for Basic Research (project # 14-04-00044).

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Appendix 1. List of taxa and characters

Recent taxa

1 *Amborella* (= Amborellaceae)
2 *Cabomba* (Cabombaceae)
3 *Brasenia* (Cabombaceae)
4 *Nuphar* (Nymphaeaceae)
5 *Barclaya* (Nymphaeaceae)
6 Nymphaeoideae (= *Nymphaea*, *Victoria*, *Euryale*; Nymphaeaceae)
7 *Trithuria* (including *Hydatella*; = Hydatellaceae)
8 *Austrobaileya* (= Austrobaileyaceae)
9 *Trimenia* (including *Piptocalyx*; = Trimeniaceae)
10 *Illicium* (= Illiciaceae)
11 *Schisandra* (including *Kadsura*; = Schisandraceae)
12 *Liriodendron* (Magnoliaceae)
13 Magnolioideae (Magnoliaceae)
14 *Degeneria* (= Degeneriaceae)
15 *Galbulimima* (= Himantandraceae)
16 *Eupomatia* (= Eupomatiaceae)
17 Annonaceae
18 Myristicaceae
19 Calycanthoideae (Calycanthaceae)
20 *Idiospermum* (Calycanthaceae)
21 Atherospermataceae
22 Siparunaceae
23 *Hortonia* (Monimiaceae)
24 Monimioideae (Monimiaceae)
25 Mollinedioideae (Monimiaceae)
26 *Gomortega* (= Gomortegaceae)
27 Lauraceae
28 Hernandioideae (= *Hernandia*, *Illigera*; Hernandiaceae)
29 Gyrocarpoideae (= *Gyrocarpus*, *Sparattanthelium*; Hernandiaceae)
30 Winteraceae
31 Canellaceae
32 Saururaceae
33 Piperaceae
34 *Lactoris* (= Lactoridaceae)
35 Asaroideae (Aristolochiaceae)
36 Aristolochioideae (Aristolochiaceae)
37 *Euptelea* (= Eupteleaceae)
38 Papaveraceae
39 Lardizabalaceae
40 *Circaeaster* (Circaeasteraceae)
41 Menispermaceae
42 Berberidaceae
43 *Glaucidium* (Ranunculaceae)
44 *Hydrastis* (Ranunculaceae)
45 Core Ranunculaceae
46 *Nelumbo* (= Nelumbonaceae)
47 *Platanus* (= Platanaceae)
48 Proteaceae
49 *Tetracentron* (Trochodendraceae)
50 *Trochodendron* (Trochodendraceae)
51 Buxaceae
52 *Acorus* (= Acoraceae)
53 Tofieldiaceae
54 *Butomus* (= Butomaceae)
55 *Aponogeton* (= Aponogetonaceae)
56 *Scheuchzeria* (= Scheuchzeriaceae)
57 Araceae
58 Nartheciaceae
59 Dioscoreaceae
60 Melanthiaceae
61 *Hedyosmum* (Chloranthaceae)
62 *Ascarina* (Chloranthaceae)
63 *Sarcandra* (Chloranthaceae)
64 *Chloranthus* (Chloranthaceae)
65 *Ceratophyllum* (= Ceratophyllaceae)

Appendix 1. Continued.

Characters

Character states scored for *Pseudoasterophyllites* indicated in bold font. Uncertain scorings (e.g., 0/1) shown by indicating both states in bold font. Characters with no state in bold font are unknown (including inapplicable). See Doyle & Endress (2000, 2010, 2014) and Endress & Doyle (2009) for sources of data and discussion of decisions on scoring of characters. With the addition of a new character 48, numbers of all subsequent characters correspond to character numbers in Doyle & Endress (2010, 2014) plus one.

1 Habit (0) tree or shrub, **(1) rhizomatous, scandent, or acaulescent.**
2 Stele (0) eustele, (1) (pseudo)siphonostele, (2) monocot-type (atactostele).
3 Inverted cortical bundles (0) absent, (1) present.
4 Protoxylem lacunae (0) absent, (1) present.
5 Pith (0) uniform, (1) septate (plates of sclerenchyma).
6 Cambium (0) present, (1) absent.
7 Storied structure (in tracheids and axial parenchyma, phloem) (0) absent, (1) present. Scored as unknown (?) when secondary growth is nearly or entirely lacking.
8 Tracheary elements (0) tracheids and elements with porose pit membranes, (1) vessel members with typical perforations.
9 Vessel perforations (end-wall pits in vesselless texa) (0) scalariform, (1) scalariform and simple in the same wood, (2) simple.
10 Fiber pitting (lateral pitting of tracheids in vesselless taxa) (0) distinctly bordered, (1) minutely bordered or simple. Scored as unknown when secondary xylem is absent or fibers are replaced by pervasive parenchyma.
11 Vessel grouping (0) predominantly solitary, (1) mostly pairs or multiples.
12 Rays (0) narrow (generally not more than four cells wide), (1) wide.
13 Paratracheal parenchyma (0) absent or scanty, (1) well developed. Taxa with pervasive parenchyma scored as unknown.
14 Tangential apotracheal parenchyma bands (0) absent, (1) present. Taxa with pervasive parenchyma scored as unknown.
15 Secondary phloem (0) simple, (1) stratified (fibers in small tangential rows or bands several cells thick).
16 Sieve element plastids (0) S-type (starch), (1) PI-type, (2) PII-type.
17 Fibers or sclerenchyma in pericyclic area (including modified protophloem) of vascular bundles (0) present, (1) absent.
18 Pericyclic ring (0) separate fiber bundles with no intervening fibers or sclerenchyma, (1) more or less continuous ring of fibers and non-U-shaped sclereids, (2) ring of fibers alternating with U-shaped (hippocrepiform) sclereids, (3) continuous homogeneous ring of fibers. Taxa with no fibers or sclerenchyma scored as unknown.
19 Laticifers in stem (0) absent, (1) present.
20 Raphide idioblasts (0) absent, (1) present.
21 Phyllotaxis (0) alternate (spiral or distichous), **(1) opposite or whorled.**
22 Distichous phyllotaxis **(0) absent,** (1) on some or all branches.
23 Nodal anatomy (0) multilacunar, (1) unilacunar one-trace, (2) unilacunar two-trace, (3) trilacunar.
24 First appendage(s) on vegetative branch **(0) paired lateral prophylls,** (1) single distinct prophyll (adaxial, oblique, or lateral).
25 Leaf base **(0) nonsheathing,** (1) sheathing (half or more of stem circumference).
26 Stipules **(0) absent,** (1) adaxial/axillary, (2) interpetiolar, (3) paired cap.
27 Axillary squamules (0) absent, (1) present.
28 Leaf blade **(0) bifacial,** (1) unifacial.
29 Leaf shape (0) obovate to elliptical to oblong, (1) ovate, **(2) linear.** We define the distinction between (0) and (1) on whether the blade is widest near or above midpoint of the line from the petiole attachment to the apex (0) vs. below the midpoint (1). This differs from a definition relative to the apex and base of the whole blade (Ellis & al., 2009), and as a result the ovate state includes forms in which the whole blade is elliptical but its base is cordate or peltate (e.g., *Nelumbo*). Endress & Doyle (2009) and Doyle & Endress (2010, 2014) scored *Platanus* and Proteaceae as (0), but here we rescore both taxa as (0/1). The previous scoring of *Platanus* was retained from the treatment of Platanaceae in Doyle & Endress (2000), which included presumed Early Cretaceous stem relatives such as *Sapindopsis* and *Araliopsoides*, in which the widest part of the blade is above the midpoint. However, with the restriction of living taxa to crown groups (Endress & Doyle, 2009), this character should have been rescored based on *Platanus* only, which varies in this character. Proteaceae were scored as obovate based on the assumption that *Bellendena* (with obovate leaves) is sister to the remaining Proteaceae, in which both states occur, but *Bellendena* now appears to be sister to the subfamily Persoonioideae, which together are sister to the rest of the family (Weston, 2014), and the ancestral state in Proteaceae is ambiguous.
30 Major venation (0) pinnate with secondaries at more or less constant angle, (1) palmate (actinodromous or acrodromous) or crowded (pinnate with crowded basal secondaries, upward decreasing angle), (2) parallel (lateral veins departing at low angles from the midrib and converging and fusing apically). This and characters 31, 32, 33, and 35 are scored as unknown (inapplicable) in taxa with linear leaves with no appreciable blade, including *Pseudoasterophyllites*.
31 Fine venation (0) reticulate, (1) open dichotomous in some or all leaves.
32 Base of blade (0) not peltate, (1) peltate in some or all leaves.
33 Apex of blade (0) simple, (1) bilobed**.**
34 Leaf dissection **(0) simple,** (1) some or all leaves lobed or compound.
35 Marginal teeth (0) absent, (1) chloranthoid, (2) monimioid, (3) platanoid.
36 Stomata (predominant type on leaf) (0) paracytic, (1) laterocytic, (2) anomocytic (including actinocytic), (3) **stephanocytic** (including cyclocytic and tetracytic). Eklund & al. (2004) scored *Ascarina* as encyclocytic (= cyclocytic, with a narrow ring of small subsidiaries) and *Hedyosmum* as stephanocytic (with a ring of more weakly differentiated subsidiaries), based on Baranova (1987) and Kong (2001), but because the cyclocytic type did not occur elsewhere in their dataset and would therefore be uninformative, Doyle & Endress (2010, 2014) did not include it as a state and scored *Ascarina* as unknown. However, Carpenter (2005) interpreted stomata of both *Hedyosmum* and *Ascarina* as stephanocytic, and his figures show that they do differ only to a minor degree. We have therefore redefined the stephanocytic state to include the cyclocytic type in *Ascarina*. Carpenter (2005) also reinterpreted Nymphaeales, described as anomocytic by earlier authors (e.g., Schneider & Williamson, 1993; Williamson & Schneider, 1993), as predominantly actinocytic (with a ring of radially elongated subsidiaries), which he treated as one of several "stephanocytic types." However, many of the subsidiaries in stomata that he described as actinocytic are only slightly differentiated from ordinary epidermal cells, and we consider that the large size and radial elongation of subsidiaries in others represent a rather different sort of differentiation from ordinary epidermal cells from that seen in stephanocytic and cyclocytic stomata. We therefore follow previous authors in scoring stomata of Nymphaeales as anomocytic, redefined to include actinocytic. *Brasenia* was not scored by Doyle & Endress (2010, 2014), but because Carpenter (2005) showed that it has the same pattern as other Nymphaeales we score it as anomocytic.
37 Midrib vasculature (0) simple arc, (1) arc with adaxial plate, (2) ring.
38 Palisade parenchyma (0) absent (mesophyll homogeneous), (1) present (mesophyll dorsiventral).
39 Asterosclerids in mesophyll (0) absent, (1) present.
40 Oil cells in mesophyll (0) absent, (1) present. *Trithuria* and *Ceratophyllum* scored as unknown because of the possibility that oil cells would be lost for functional reasons in submerged aquatics and the presence of tanniniferous cells in *Ceratophyllum* (Metcalfe & Chalk, 1950) that might be modified oil cells.
41 Mucilage cells in mesophyll (0) absent, (1) present. *Trithuria* and *Ceratophyllum* scored as unknown for reasons given for character 40.
42 Inflorescence (0) solitary flower (or occasionally with 1–2 lateral flowers), (1) botryoid, panicle, or thyrsoid (monotelic), **(2) raceme, spike, or thyrse** (polytelic). In taxa with unisexual flowers, scoring is based on the sex with the more complex inflorescences.
43 Inflorescence partial units **(0) single flowers,** (1) cymes.
44 Inflorescence (or partial inflorescence) **(0) not modified**, (1) modified into globular head.
45 Pedicel (0) present in some or all flowers, **(1) absent or highly reduced** (flower sessile or subsessile).
46 Floral subtending bracts **(0) present,** (1) present in female, absent in male flowers, (2) absent in all flowers.
47 Sex of flowers (0) bisexual, **(1) unisexual.** Taxa with both bisexual and unisexual flowers on the same plant (polygamous) are scored

Appendix 1. Continued.

as (0/1). Hernandiaceae were treated as a single taxon in Doyle & Endress (2000) but split into Hernandioideae (*Hernandia*, *Illigera*) and Gyrocarpoideae (*Gyrocarpus*, *Sparattanthelium*), which are sister groups, in Endress & Doyle (2009) and Doyle & Endress (2010, 2014). *Hernandia* has unisexual flowers, but because *Illigera* and *Sparattanthelium* have bisexual flowers and *Gyrocarpus* is polygamous (Kubitzki, 1993), Doyle & Endress (2000) scored the family as bisexual, the inferred ancestral condition. However, this character was inadvertently not reanalyzed when the family was split. Given the relationships of the four genera and our treatment of polygamous as (0/1), we retain the scoring of Gyrocarpoideae as bisexual, but we rescore Hernandioideae as (0/1).

48 Inflorescences of unisexual flowers (0) both sexes with more than one flower, **(1) male with more than one flower, female with one flower** (uniflorous, solitary). Bisexual taxa scored as unknown. No taxa in the present dataset have solitary male and female flowers; if such taxa existed, they would be scored as unknown, since the state would already be expressed in the main inflorescence character (42).

49 Floral base (0) hypanthium absent, superior ovary, (1) hypanthium present, superior ovary, (2) partially or completely inferior ovary. Scored as unknown in flowers consisting of one carpel, including *Pseudoasterophyllites*. Endress & Doyle (2009) and Doyle & Endress (2010, 2014) scored *Sarcandra* and *Chloranthus* as unknown, but because the attachment of the stamen or tripartite androecium to the back of the carpel is comparable to the attachment of the stamens in *Canrightia* (which has a reduced perianth adnate to the ovary) and sufficiently consistent with the usual definition of an inferior ovary we have followed Friis & al. (2015) in rescoring them as (2).

50 Floral receptacle (female portion) **(0) short,** (1) elongate.

51 Pits in receptacle bearing individual carpels **(0) absent,** (1) present.

52 Cortical vascular system (0) absent or supplying perianth only, (1) supplying androecium, (2) supplying androecium plus gynoecium.

53 Floral apex (0) used up after production of carpels, (1) protruding in mature flower. Unicarpellate taxa scored as unknown.

54 Perianth (0) present, **(1) absent.** Characters 55–61 scored as unknown (inapplicable) in taxa with no perianth.

55 Perianth phyllotaxis (0) spiral, (1) whorled.

56 Perianth merism (0) trimerous, (1) dimerous, (2) polymerous. Taxa with spiral perianth phyllotaxis scored as unknown.

57 Perianth whorls (series when phyllotaxis is spiral) (0) one, (1) two, (2) more than two. Includes petals (character 58).

58 Tepal differentiation (0) all more or less sepaloid; (1) outer sepaloid, inner distinctly petaloid; (2) all distinctly petaloid. Does not include petals (58).

59 Petals (0) absent, (1) present. Taxa with no perianth or only one whorl or series scored as unknown.

60 Nectaries on inner perianth parts (0) absent, (1) present.

61 Outermost perianth parts (0) free, (1) at least basally fused.

62 Calyptra derived from last one or two bracteate organs below the flower **(0) absent,** (1) present.

63 Stamen number (0) more than one, **(1) one.** Characters 64–69 scored as unknown (inapplicable) in taxa with one stamen.

64 Androecium phyllotaxis (0) spiral, (1) whorled.

65 Androecium merism (0) trimerous, (1) dimerous, (2) polymerous. Taxa with spiral androecium phyllotaxis scored as unknown.

66 Number of stamen whorls (series when phyllotaxis is spiral; includes inner staminodes) (0) one, (1) two, (2) more than two. *Ascarina* was scored as having one whorl in Endress & Doyle (2009) and Doyle & Endress (2010, 2014), but because we know of no data on stamen arrangement in those species with more than one stamen we have rescored the genus as unknown.

67 Stamen positions (0) single, (1) double (at least in outer whorl). Because double positions are defined with reference to a preceding whorl, taxa with no perianth and one whorl of stamens are scored as unknown. *Ascarina*, which has no perianth, was mistakenly scored as (0) in Endress & Doyle (2009) and Doyle & Endress (2010, 2014); we have rescored it as unknown.

68 Stamen fusion (0) free, (1) connate.

69 Inner staminodes (0) absent, (1) present. Taxa with one whorl of stamens scored as unknown. Doyle & Endress (2014) inadvertently scored *Canrightia*, which has one whorl of stamens, as (0); we have rescored it as unknown.

70 Glandular food bodies on stamens or staminodes **(0) absent,** (1) present.

71 Stamen base **(0) short** (2/3 or less the length of anther), (1) long (>2/3 length of anther) and wide (>1/2 width of anther), (2) long (2/3 or more length of anther) and narrow (<1/2 width of anther) (typical filament).

72 Paired basal stamen glands **(0) absent,** (1) present.

73 Connective apex **(0) extended,** (1) truncated or smoothly rounded, (2) peltate.

74 Pollen sacs (0) protruding, **(1) embedded**.

75 Microsporangia **(0) four**, (1) two.

76 Orientation of dehiscence (0) distinctly introrse, **(1) latrorse to slightly introrse,** (2) extrorse.

77 Mode of dehiscence **(0) longitudinal slit,** (1) H-valvate, (2) valvate with upward-opening flaps.

78 Connective hypodermis (0) unspecialized, (1) endothecial or sclerenchymatous.

79 Tapetum (0) secretory, (1) amoeboid.

80 Microsporogenesis (0) simultaneous, (1) successive.

81 Pollen nuclei (0) binucleate, (1) trinucleate.

82 Pollen unit **(0) monads,** (1) tetrads.

83 Pollen size (average) (0) large (> 50 µm), **(1) medium** (20–50 µm), (2) small (< 20 µm); ordered.

84 Pollen shape (0) boat-shaped, **(1) globose,** (2) triangular, angulaperturate.

85 Aperture type **(0) single** (presumably polar, including monosulcate and monoporate) or disulcate (one furrow at each pole), (1) inaperturate, (2) sulculate, (3) (syn)tricolpate with colpi arranged according to Garside's law, with or without alternating colpi, (4) tricolpate.

86 Single aperture shape **(0) elongate,** (1) round. This and the following character are scored as unknown in taxa with more than one aperture.

87 Single aperture branching **(0) unbranched,** (1) with several branches.

88 Infratectum (0) granular (including "atectate"), **(1) intermediate,** (2) columellar; ordered.

89 Tectum **(0) continuous or microperforate,** (1) perforate (foveolate) to semitectate (reticulate), (2) reduced (not distinguishable from underlying granules).

90 Grading of reticulum (0) uniform, (1) finer at ends of sulcus (liliaceous), (2) finer at poles (rouseoid). Scored only in taxa with state (1) in character 88.

91 Striate muri **(0) absent,** (1) present.

92 Supratectal spinules (smaller than the width of tectal muri in foveolate-reticulate taxa; includes rounded as well as pointed elements) (0) absent, **(1) present.**

93 Prominent spines (larger than spinules, easily visible with light microscopy) **(0) absent,** (1) present.

94 Aperture membrane (0) smooth, **(1) sculptured.**

95 Extra-apertural nexine stratification (0) foot layer, not consistently foliated, no distinctly staining endexine or only problematic discontinous traces, **(1) foot layer and distinctly staining, continous endexine,** or endexine only, (2) all or in part foliated, not distinctly staining.

96 Nexine thickness (0) absent or discontinuous traces, **(1) thin but continuous,** (2) thick (1/3 or more of total exine); ordered.

97 Carpel number **(0) one,** (1) 2–5 in one whorl or series (when phyllotaxis is spiral), (2) more than 5 in one whorl or series, (3) more than one whorl or series.

98 Carpel form (0) ascidiate up to stigma, (1) intermediate (both plicate and ascidiate zones present below the stigma) with ovule(s) in the ascidiate zone, (2) completely plicate, or intermediate with some or all ovule(s) in the plicate zone.

99 Postgenital sealing of carpel (0) none, (1) partial, (2) complete.

100 Secretion in area of carpel sealing (0) present, (1) absent.

101 Pollen tube transmitting tissue (0) not prominently differentiated, (1) one cell layer prominently differentiated, (2) more than one cell layer prominently differentiated.

102 Style **(0) absent** (stigma sessile or capitate), (1) present (elongated, distinctly constricted apical portion of carpel).

103 Stigma **(0) extended** (half or more of the style-stigma zone), (1) restricted (above slit or around its upper part).

104 Multicellular stigmatic protuberances or undulations **(0) absent**, (1) present.

105 Stigmatic papillae (most elaborate type) (0) absent, (1) unicellular

Appendix 1. Continued.

or with a single emergent cell and one or more small basal cells, (2) uniseriate pluricellular with emergent portion consisting of two or more cells.
106 Extragynoecial compitum (0) absent, (1) present. Unicarpellate taxa scored as unknown (inapplicable).
107 Carpel fusion (0) apocarpous, (1) parasyncarpous, (2) eusyncarpous (at least basally). Taxa with one carpel scored as unknown (inapplicable).
108 Oil cells in carpels (0) absent or internal, (1) intrusive. Taxa with no oil cells in any tissue of the plant scored as unknown.
109 Long unicellular hairs on and/or between carpels (0) absent, (1) present. This and the following three characters are usually not scored in fossils.
110 Short curved appressed unlignified hairs with up to two short basal cells and one long apical cell on carpels (0) absent, (1) present.
111 Nectary on dorsal or lateral sides of carpel or pistillode (0) absent, (1) present.
112 Septal nectaries or potentially homologous basal intercarpellary nectaries (0) absent, (1) present.
113 Number of ovules per carpel **(0) one,** (1) two or varying between one and two, (2) more than two.
114 Placentation (0) ventral, (1) laminar-diffuse or "dorsal."
115 Ovule direction **(0) pendent,** (1) horizontal, (2) ascendent.
116 Ovule curvature (0) anatropous (or nearly so), **(1) orthotropous** (including hemitropous).
117 Integuments (0) two, (1) one.
118 Outer integument shape (0) semiannular, (1) annular. Orthotropous taxa scored as unknown.
119 Outer integument lobation (0) unlobed, (1) lobed.
120 Outer integument thickness (at middle of integument length) (0) two cells, (1) two and three to four, (2) four and five, or more; ordered.
121 Inner integument thickness (0) two cells, (1) two and three, or three, (2) three and more; ordered.
122 Chalaza (0) unextended, (1) pachychalazal, (2) perichalazal. Orthotropous taxa scored as unknown.
123 Nucellus (0) crassinucellar (including weakly so), (1) tenuinucellar or pseudocrassinucellar.
124 Fruit wall (0) wholly or partly fleshy, (1) dry.
125 Lignified endocarp (0) absent, (1) present. Applicable only in fleshy fruits; taxa with dry fruit wall scored as unknown.
126 Fruit dehiscence **(0) indehiscent** or dehiscing irregularly, dorsally only, or laterally, (1) dehiscent ventrally or both ventrally and dorsally, (2) horizontally dehiscent with vertical extensions.
127 Hooked hairs on fruit **(0) absent,** (1) present.
128 Testa (0) slightly or non-multiplicative, (1) multiplicative. Because this character is defined by comparison with the number of cell layers in the ovule stage, it is not scored in fossils.
129 Exotesta **(0) unspecialized,** (1) palisade or shorter sclerotic cells, (2) tabular, (3) longitudinally elongated, more or less lignified cells.
130 Mesotesta lignification (0) unlignified, (1) with sclerotic layer, (2) with fibrous layer. This and the following character are scored as unknown (inapplicable) in taxa with a 2-layered outer integument.
131 Mesotesta fleshiness (0) not juicy, (1) wholly or partly modified into a juicy sarcotesta.
132 Endotesta (0) unspecialized, (1) single layer of thin-walled cells with fibrous endoreticulum, (2) multiple layer of thin-walled cells with fibrous endoreticulum, (3) tracheidal, (4) palisade of thick-walled cells.
133 Tegmen (0) unspecialized, **(1) thick-walled endotegmen** (and ectotegmen if present), (2) fibrous to sclerotic exotegmen.
134 Ruminations (0) absent, (1) testal, (2) tegminal and/or chalazal.
135 Operculum (0) absent, (1) present.
136 Aril (0) absent, (1) present.
137 Female gametophyte (0) four-nucleate, (1) eight- or nine-nucleate. Tetrasporic types scored as unknown.
138 Endosperm development (0) cellular, (1) nuclear, (2) helobial.
139 Endosperm in mature seed (0) present, (1) absent.
140 Perisperm (0) absent, (1) from nucellar ground tissue, (2) from nucellar epidermis.
141 Embryo (0) minute (less than 1/2 length of seed interior), (1) large.
142 Cotyledons (0) two, (1) one.
143 Germination (0) epigeal, (1) hypogeal.

Vol. 65 (6) • December 2016

TAXON

International Journal of Taxonomy, Phylogeny and Evolution

Electronic Supplement to

Pseudoasterophyllites cretaceus from the Cenomanian (Cretaceous) of the Czech Republic: A possible link between Chloranthaceae and *Ceratophyllum*

Jiří Kvaček, James A. Doyle, Peter K. Endress, Véronique Daviero-Gomez, Bernard Gomez & Maria Tekleva

Taxon 65

Table S1. Data matrix.

A = 0/1, B = 0/2, C = 0/3, D = 0/4, E = 1/2, F = 1/3, G = 2/3, H = 0/1/2

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                    ---------1---------2---------3---------4---------5---------6---------7---------8---------9---------0---------1---------2---------3---------4---
                    12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123
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Cabomba             100101?00??????01?10A12000?0111110102?1000200000?000000101?1100100010?020100200010000000020?1A0111110000100100?0100210000010001?000100000100201100?
Brasenia            100101?00????????1?10012?000011010002010000?000?0?000000010l2?000010210002010010000100000002O?0001113000?100100?0100110000??10??1?000100000010?201001
Nuphar              10?101?00??????01?10003100?0110000002?1100200000?0?000000102110000122100000210010000A0000000102?0111112020000011?2?000021000000200000001000001100001001
Barclaya            10?101?00??????01?1000???00?0110000??1100200002?0?2000001221000001222?000000100000??00112??20?000???212000000212?0100210?10?000?000000???000100000101
Nymphaeoideae       100101?00??????01?10003101001100000?2?1100200020?2000101221000001222?000100100000A0012??10?000?122020000021?2?0100210000A0E0A0000001000001100001001
Trithuria           1??101??0??????01?0000?000000?????0?2?00??2100210?000?1??????01?????0201?0100??002000020?010?0100??0?02???0100?000??00001?0001??000100001?1
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Trimenia            A00000010AAA0000010010200?0A000001000011100A0A00000?00?20000000?E000020000E000000112??2100101111000000012??A0A000000000121000000001100000?00?00000?
Illicium            0100000100000000000000010000000000000001111100000?0000100?21000000?E000010100000000001132?2100001111211011001101000000200112E001?10A1100000000000000
Schisandra          1100000011000000001000010000?0000000010001111B000010010000002100000?H0100101100B000000113??2100001111300010001101000010000A2100000001100000000000000
Liriodendron        0000100101100011A000000001300000010001101000000?0102001021000100?2000000011020?000000000020?0000213220011010000000101000021001?001010200001000000
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Degeneria           0000100101110111000001010000000000001001000000000?0001000?2101000?2001100010210000000000000?0000?0022110002??000002010010210001010012010010000000
Galbulimima         000010011A1001100100031300000000000001?0100000000?01010?????????100?2001100010210010011000000?0000?032?0101011100??000001001021000100000100?001?00000
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Calycanthoideae     0110000121100001020010200000100000000000100000000?1000000?21000000?2001A0000002000A0112??2100000213221011011001000102000012200l?0010003000010101100
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Platanus            0000000011001000001000101111?0A100013111000E01121000000001B10000001B00000002A0111000011 4???2100001123221110010O???0010010?112?01?000010000001100 100
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Asteropollis plant  ?????????????????????????????????????????????2??1E1?200??0100A??101?????????0001101 0????0110012100101??0?????1?????????????0??1?????????00?????????????????
Appomattoxia        ?????????????????????????????????????????????????????????????????????????????????????????????100?0????0E100010?0101112?????00?1????????0?01????????1?01?0???100?????????
                    ---------1---------2---------3---------4---------5---------6---------7---------8---------9---------0---------1---------2---------3---------4---
                    12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123
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